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THE GENUS *UPEROLEIA* GRAY (ANURA: LEPTODACTYLIDAE) IN QUEENSLAND, AUSTRALIA

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Abstract: Four new taxa are described: *U. capitulata* sp. nov. from south-western Queensland and north-western N.S.W., *U. fusca* sp. nov. from northern coastal N.S.W. to the central Qld coast, *U. littlejohni* sp. nov. from north-central Qld and *U. mimula* sp. nov. from Cape York.

Uperoleia trachyderma Tyler, Davies and Martin and *U. inundata* Tyler, Davies and Martin are recorded from Queensland for the first time. The distribution of *U. lithomoda* Tyler, Davies and Martin is expanded and the morphology and osteology of the species are examined across its range. Previous descriptions of these taxa are supplemented with osteological data on the carpus, tarsus and ilium, and with descriptions of the hyoid.

A generic checklist and keys to species in Australia are provided.

The nomenclature of frogs of the genus *Uperoleia* Gray has been in a state of flux since the revision of Tyler, Davies and Martin (1981a) who showed the genus to comprise many more than the three named species [*Uperoleia marmorata* Gray, *U. rugosa* (Andersson) and *U. mjobergi* (Andersson)] recognised by earlier workers (Littlejohn 1967, Lynch 1971, Cogger 1975, Tyler 1976).

Tyler *et al.* (1981a,b,c) and subsequently Davies *et al.* (1985) were concerned mainly with species from the north and north-west of the continent, leaving the eastern Australian fauna largely unknown. Davies and Littlejohn (1986) amplified the redescriptions of *U. laevigata* Keferstein of Tyler *et al.* (1981a) and of *U. rugosa* of Tyler *et al.* (1981a) and Davies and McDonald (1985). They referred *U. fimbrianus* (Parker) to the synonymy of *U. rugosa* and described *U. tyleri* and *U. martini* from coastal N.S.W. and Victoria. A fourth species of *Uperoleia* has been reported from northern Queensland, namely *U. lithomoda* Tyler, Davies and Martin (Tyler & Davies 1984).

Our studies have revealed the occurrence of a further six species of *Uperoleia* in Queensland; four of these are undescribed. Here we describe the four new taxa, report range extensions of two species of *Uperoleia* into Queensland and supplement their descriptions, and provide additional data on the distribution and morphology of *U. lithomoda*.

MATERIALS AND METHODS

Material reported here is deposited in the American Museum of Natural History, New York (AMNH), Australian Museum, Sydney (AM), CSIRO Wildlife Collection, Canberra (ANWC), British Museum (Natural History), London (BMNH), Californian Academy of Sciences, San Francisco (CAS), Museum of Comparative Zoology, Harvard (MCZ), Museum of Natural History, University of Kansas, Lawrence (KU), Museum of Victoria, Melbourne (NMV), Northern Territory Museum, Darwin (NTM), Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAM) and the University of Adelaide osteological collection (UAZ). Initials following these acronyms are departmental identifications within the institutions and generally precede the registration numbers on the tags attached to the specimens.

Most species of *Uperoleia* possess parotoid glands which cover the side of the head and obscure the tympana, and hence prevent accurate measurement of head length and head width. Measurements taken were: eye diameter (E), eye to naris distance (E-N), internarial span (IN), snout to vent length (S-V) and tibia length (TL). The methods of measurement follow Tyler (1968). Data are presented as mean ± standard deviation with ranges in parentheses.

Osteological data were obtained from specimens cleared and stained with alizarin red S for bone after the method of Davis and Gore (1947), and with alizarin red S for bone and alcian blue for cartilage after the method of Dingerkus and Uhler (1977). Osteological descriptions follow Trueb (1979) and Andersen (1978) (for the carpus and tarsus).

Mating calls were recorded with a Uher 4000 Report Monitor tape recorder and an AKG D190 ES microphone, or a Sony TC510-2 tape recorder and a Beyer M88 dynamic microphone at a tape speed of 19 cm sec^{-1}. Wet bulb air temperatures were measured with a Schultheis rapid-reading thermometer close to the calling sites of males. Calls were analysed by means of a sound spectrograph (Kay Model 7800 digital Sona-Graph). Temporal characteristics of calls were determined from wide-band (300 Hz bandpass) and spectral characteristics from narrow band (45 Hz bandpass) spectrograms. Three calls of each male were analysed and mean values were calculated.

Line drawing outlines were made with the aid of a Wild M9 stereoscopic dissecting microscope with a 0.4× reducing lens, and a camera lucida. Vegetation descriptions follow Walker and Hopkins (1984).

Statistical analyses of morphological measurements follow Sokal and Rohlf (1981).

SYSTEMATIC ZOOLOGY

Uperoleia lithomoda Tyler, Davies and Martin

Uperoleia lithomoda Tyler, Davies & Martin 1981, Aust. J. Zool. Suppl. Ser. 79, p. 43.

Uperoleia variegata Tyler, Davies & Martin 1981a, p. 55.

Uperoleia lithomoda: Cogger 1983, p. 84; Cogger, Cameron & Cogger 1983, p. 33; Tyler & Davies 1984, p. 123 (part.); Tyler, Smith & Johnstone 1984, p. 99; Tyler 1985, p. 407; Tyler & Davies 1986, p. 59; Tyler, Davies & Watson 1986, p. 98; Tyler, Davies & Watson in press; Mahony & Robinson 1986, p. 120.

DEFINITION: A small species (males 19-26 mm S-V, females 17-30 mm S-V) of moderately-gross habitus and short limbs. Maxillary teeth absent; frontoparietal fontanelle poorly to moderately exposed; basal or no webbing between the toes; toes poorly to moderately fringed; eye to naris distance usually greater than internarial span; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Mating call an explosive tick of 4-6 pulses with a pulse repetition rate of 250-450 pulses sec^{-1}.

MATERIAL EXAMINED: W.A.: SAM R28741-3, swamp at spillway bridge, 11.5 km NE Lake Argyle Tourist Village (16°02′, 128°47′); SAM R28744-56, WAM R94346-47, Gibb River Station in billabong behind Hstd; SAM R28757, WAM R94348-50, Gibb River Rd, 22.1 km NW Lennard River.

N.T.: AM R53619-20, 15 km N McArthur River Camp on Borroloola Rd (16°15′, 136°04′); R53352, 36.5 km N McArthur River Camp on Borroloola Rd (16°16′, 136°07′); R53693, 10 km N McArthur River Camp on Borroloola Rd; R53732-5, approx. 15 km N McArthur River Camp on Borroloola Rd (16°15′, 136°04′); SAM R25110-11, 10.2 km from Katherine along Gorge Rd; R20447, 15 km from Katherine along Gorge Rd; R24010, 408 km W Katherine on Victoria Hwy; R24011-14, 11 km NE Katherine along Gorge Rd; R24015-16, Saddle Creek, Victoria Hwy; R25108-9, 17 km E Roper River Rd/Stuart Hwy Jen; R28758-61, 7 km W Mary River on Arnhem Hwy; R28762-64, Mary River Bridge, Arnhem Hwy; R25467-71, 2.7 km E Angurugu, Groote Eylandt; R27473, 8.2 km E Emerald River, Groote Eylandt.

Qld: NTM R11741, R11747, R11756-7, R11760, R11763, R11765 Westmoreland; SAM R28765-7, R29691-5, QM J45922, Kangaroo Rat Mine, Amber Station; SAM R28768, 1.6 km from Burlington Station on Amber Station Rd; SAM R28769, Amber Station near Lynd River Crossing (formerly QNPWS N28751); SAM R28770, James Cook University Experimental Farm "Fletcherview", Charters Towers; SAM R28771, Lakefield National Park Ranger Station (formerly QNPWS 28872); SAM R28773-5, QM J45997, J45988-91, UAZ A897 (formerly QNPWS 32319), Coen Airport (13°45′30″, 143°06′30″); SAM R28772, Twin Humps, 12 km N Coen (13°51′30″, 143°9′30″); QM J31554, Chillagoe; J19862, 1.6 km S Yorkeys Knob P.O.; J29859, 62 km from Townsville on Charters

TABLE 1

SNOUT-VENT LENGTH, TIBIA LENGTH/SNOUT-VENT LENGTH AND EYE-NARIS DISTANCE/INTERNARIAL SPAN MEASUREMENTS FOR SEVERAL POPULATIONS OF *Uperoleia lithomoda*. DATA ARE EXPRESSED AS MEAN ± STANDARD DEVIATION WITH RANGES IN PARENTHESES. DATA FOR MALES AND FEMALES ARE POOLED FOR RATIO CALCULATIONS.

		Gibb River Station W.A.	22.1 km NW Lennard River W.A.	Spillway Swamp W.A. (type locality)	Katherine N.T.	Mary River N.T.	McArthur River N.T.	Groote Eylandt N.T.	Edward River Qld	Amber Stn/ Charters Towers Qld	All material examined
S-V	n	14	6	4	15	7	8	10	26	12	102
	♂♂	20.25 ± 1.08	22.83 ± 1.37	19.0	20.92 ± 1.66	18.76 ± 1.10	21.18 ± 1.24	24.6 ± 1.90	16.89 ± 0.76	21.9 ± 1.78	20.22 ± 2.67
		(17.9 -22.1)	(21.5-25.1)	(17.8-20.5)	(18.85-23.5)	(16.7-20.1)	(19.4-22.7)	(20.0-26.5)	(16-17.9)	(18.3-24.5)	(16-26.5)
	n	3			2			1	4		10
	♀♀	22.3						29.5	18.58		21.76 ± 3.77
		(20.3-23.6)			(19.5-24.5)				(16.8-19.2)		(16.8-29.5)
TL/S-V		0.35 ± .02	0.35 ± .02	0.36	0.34 ± .02	0.35 ± .02	0.33 ± .02	0.36 ± .03	0.36 ± .02	0.37 ± .02	0.35 ± .02
		(0.31-0.39)	(0.32-0.37)	(0.34-0.39)	(0.31-0.37)	(0.34-0.40)	(0.31-0.37)	(0.32-0.44)	(0.31-0.41)	(0.33-0.42)	(0.31-0.42)
E-N/IN		1.27 ± .18	1.33 ± .17	1.13	1.35 ± .25	1.44 ± .28	1.35 ± .23	1.25 ± .17	1.23 ± .19	1.20 ± .20	1.28 ± .22
		(1.00-1.64)	(1.13-1.57)	(1.00-1.31)	(0.94-1.75)	(1.13-1.89)	(1.13-1.85)	(1.00-1.53)	(0.83-1.60)	(0.95-1.53)	(0.83-1.89)

Towers Rd; J29884, 96 km from Townsville on Charters Towers Rd; SAM R24349 (24), 1 km E Edward River Township; R24343-8, Edward River Township; SAM R28776, R29696, QM J45993, Pajingo Station (146°11′, 20°47′); SAM R28777-9, R29697, QM J45994, Battery Station, Snake Creek (145°39′, 19°27′); SAM R28780, QM J45995, Occupation licence 117 (145°13′, 20°40′); QM J45996, Lockwall Station (145°51′, 19°54′); QM J42533, J42536, 20 km W Cooktown; QM J38842-56, Pentland, N side of town; J38874-75, 18 km W Torrens Creek; AM R38449-54, Rocky Creek, 40 km S Batavia Downs, Cape York.

External Morphology: The specimens were arbitrarily divided into eight populations on a geographic basis: Gibb River, W.A., Lennard River environs, W.A., Katherine area, N.T., Mary River (Arnhem Hwy) area, N.T., Groote Eylandt, N.T., McArthur River area, N.T., Edward River township, Qld, and Amber Station area, Qld. Measurements from these populations are shown in Table 1.

An F_{max} test for homogeneity of variances is not significant and a one way analysis of variance of size is highly significant ($F = 46.25$) indicating size differences between different populations. A GT_2 method of multiple comparison amongst pairs of means based on unequal sample sizes gave results depicted in Table 2. There is no geographic cline in these data.

The shape of the snout can vary from moderately truncate to quite sharply pointed even within one population (Fig. 1). The sharply-pointed snouts (Fig. 1C) are not common and within any population about equal proportions of blunt and gently-rounded snouts occur. The exception is in the Gibb River Station population where more blunt-snouted specimens were observed. Within this sample are the paratypes of *U. variegata* Tyler Davies and Martin referred to the synonymy of *U. lithomoda* by Tyler *et al.* (in press). These specimens were collected in the dry season from underground and appear to have been preserved in strong fixative. They are somewhat dehydrated and distortion of snout shape has occurred (see Davies & Littlejohn 1986). The higher proportion of blunt-snouted individuals in this population thus may be an artifact. The nostrils are usually located dorsolaterally but are occasionally almost dorsal.

Rugosity of the dorsum is usually moderate (Fig. 2) except in material collected in the dry season (e.g. Gibb River and McArthur River) when equal proportions of moderately- and poorly-rugose dorsa are recorded. Parotoid glands are always well developed (Fig. 2). Inguinal glands also are well developed except in most of the *U. variegata* paratypes collected in the dry season, presumably when glandular activity is minimal (see McDiarmid 1968). Coccygeal glands are usually well, or occasionally moderately developed, except, again, in the dry season Gibb River material in which these glands are poorly developed.

The pattern of the dorsum of *U. lithomoda* is usually strongly defined. Ground colour is usually grey with brown or black markings often highlighted with rust-coloured spots. Dark ereseentie markings are usually medial to the parotoid glands in the seapular area and are often raised in the form of lyrate plicae (Fig. 3). Seapular plicae are present except in the Edward River and Gibb River populations in which they are absent in a third of individuals. Gold colouring on the dermal glands produces yellow-gold lateral stripes in most specimens (Fig. 2).

Subarticular and palmar tubercles on the hand are usually prominent, or moderately prominent. The presence of supernumerary tubercles on the hand varies. The palmar tubercle at the base of the thumb is generally small and masked by the unpigmented nuptial pad in most males.

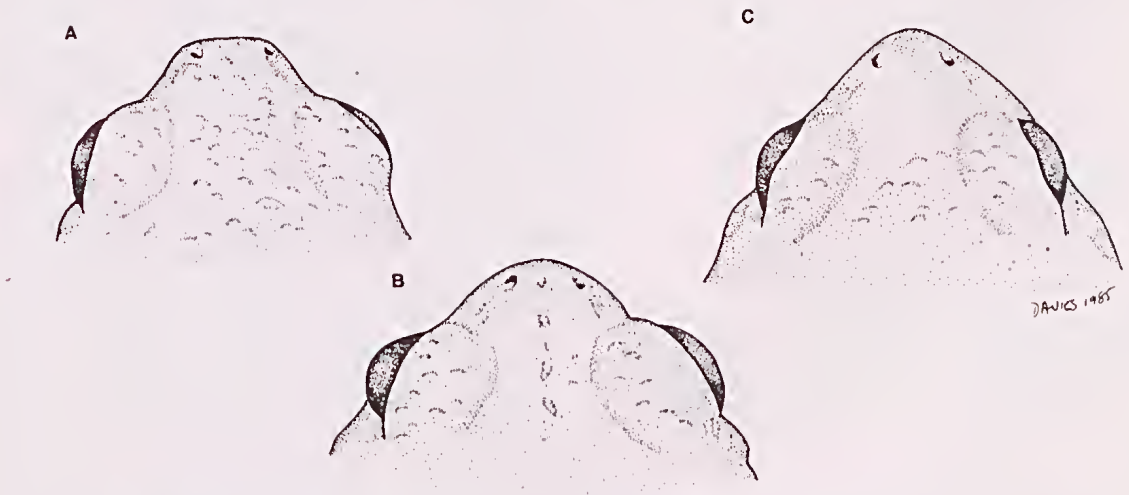

Fig. 1 – Dorsal views of the heads of *Uperoleia lithomoda* from Gibb River Station, W.A. A, blunt. B, rounded C, sharp.

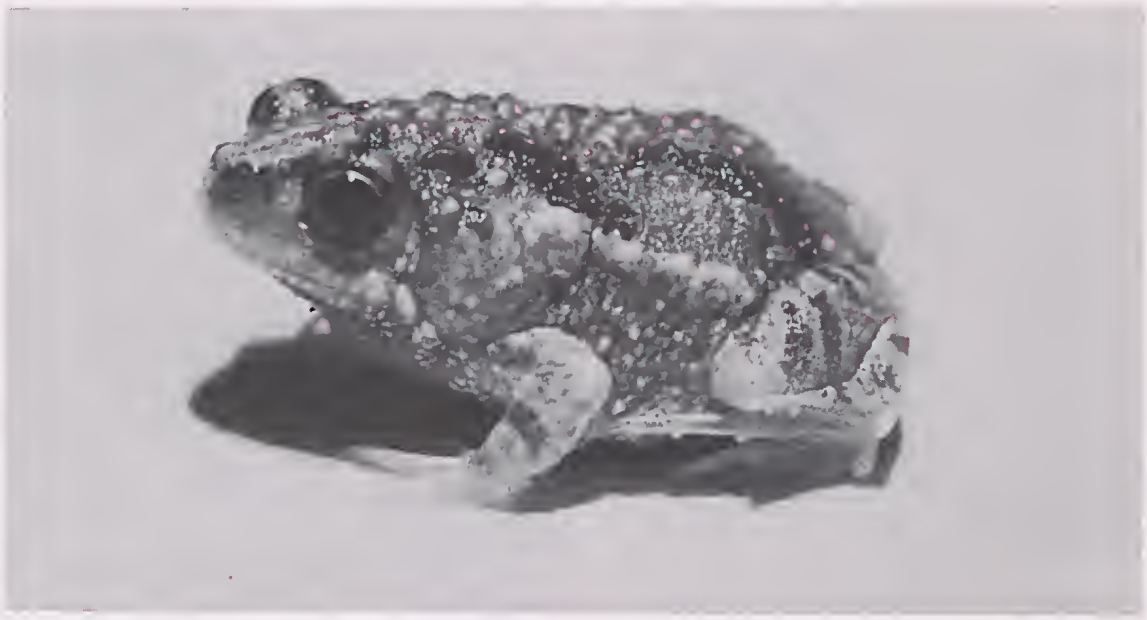

Fig. 2—*Uperoleia lithomoda* in life (Katherine, N.T.).

Fig. 3—Dorsal pattern in *Uperoleia lithomoda* (SAM R25468).

Fringing on the toes ranges from poor to moderate. Preservation influences this feature; freshly- and carefully-preserved material tends to have more pronounced fringing than less well-preserved material. In most populations moderately fringed toes are typical except for the Mary River and Edward River populations. Toe webbing is either absent, or basal, usually in about equal proportions. In the Edward River populations, however, 27 of 30 specimens lacked toe webbing. Variation in toe webbing and fringing is shown in Fig. 4. Both inner and outer metatarsal tubercles are particularly prominent in *U. lithomoda* (Figs. 2, 4). The outer metatarsal tubercle is usually aligned in a plane perpendicular to the long axis of the foot, occasionally slightly angled. Subarticular tubercles are conical and not very prominent.

The ventral skin is usually highly granular except in material collected in the dry season at Gibb River, and in some of the material collected at this site at the beginning of the wet season. Granularity is less prominent in the few females examined, than in males. White flecks often are present in the centre of the granules. Ventral pigmentation is rare other than on the throat in calling males. If present, it is in the form of a faint dusting of individual pigment granules usually visible only with a microscope. Groote Eylandt and Edward River material shows greater ventral pigmentation than other specimens. Inguinal patches are not always apparent. When present, they are not as prominent as femoral patches. A faint or moderately-developed midvertebral stripe is almost always present.

TABLE 2

MULTIPLE COMPARISONS AMONGST PAIRS OF MEANS OF SNOUT-VENT LENGTH OF *Uperoleia lithomoda* AT EIGHT LOCALITIES, BASED ON UNEQUAL SAMPLE SIZES—GT_2 METHOD. THE DIFFERENCES SIGNIFICANT AT THE 5% LEVEL ARE INDICATED BY AN ASTERISK. Localities are as follows: 1 Edward River, Qld; 2 Mary River, N.T.; 3 Gibb River, W.A.; 4 Katherine and environs, N.T.; 5 McArthur River environs, N.T.; 6 Amber Station environs, Qld; 7 Lennard River environs, W.A.; 8 Groote Eylandt, N.T.

Ranked localities	1	2	3	4	5	6	7	8
1	—	2.277	1.7727	1.7337	2.1621	1.8664	2.4217	1.8664
2	1.87	—	2.4753	2.4479	2.7674	2.5433	2.9749	2.6352
3	3.36*	1.49	—	1.3807	2.370	2.1037	2.6093	2.214
4	4.03*	2.16	0.67	—	2.3414	2.0715	2.5818	2.1832
5	4.29	2.42	0.93	0.26	—	1.5441	2.8879	2.5365
6	5.01*	3.14*	1.65	0.98	0.72	—	2.674	2.2897
7	5.94*	4.07	2.58	1.91	1.65	0.93	—	2.7613
8	7.71*	5.84*	4.35*	3.68*	3.42*	2.70*	1.77	—

OSTEOLOGY: *Material examined*: W.A.: SAM R17220, Granite Creek, 14.1 km NE Lake Argyle Tourist Village (Paratype); UAZ A769, A808, Spillway Bridge Swamp 11.5 km N Lake Argyle Tourist Village (Topotypes); SAM R17219, Gibb River Hstd garden; UAZ A767-8, A781-98, Swamp behind Gibb River Station Hstd billabong; UAZ A780, B896, 22.1 km NW Lennard River on Gibb River Rd.

N.T.: SAM R17218, Arnhem Hwy at Fogg Dam turnoff, 24 km ESE Darwin; UAZ A809, Mary River Bridge on Arnhem Hwy; UAZ A807, 6.4 km N Katherine along Gorge Rd; UAZ A799-806, A811, B812, 2.7 km E Angurugu, Groote Eylandt, ANWC A1085, Elcho Island.

Qld: UAZ A897 (formerly QNPWS N32319), Coen Airport; UAZ A810, Edward River township; SAM R29691-2, Kangaroo Rat Mine, Amber Station; SAM R28771, Lakefield Ranger Station; AMR 38450, Rocky Creek, 32 km S Batavia Downs; QM J31554, Chillagoe; J19862, 1.6 km S Yorkeys Knob P.O.; J29859, 62 km

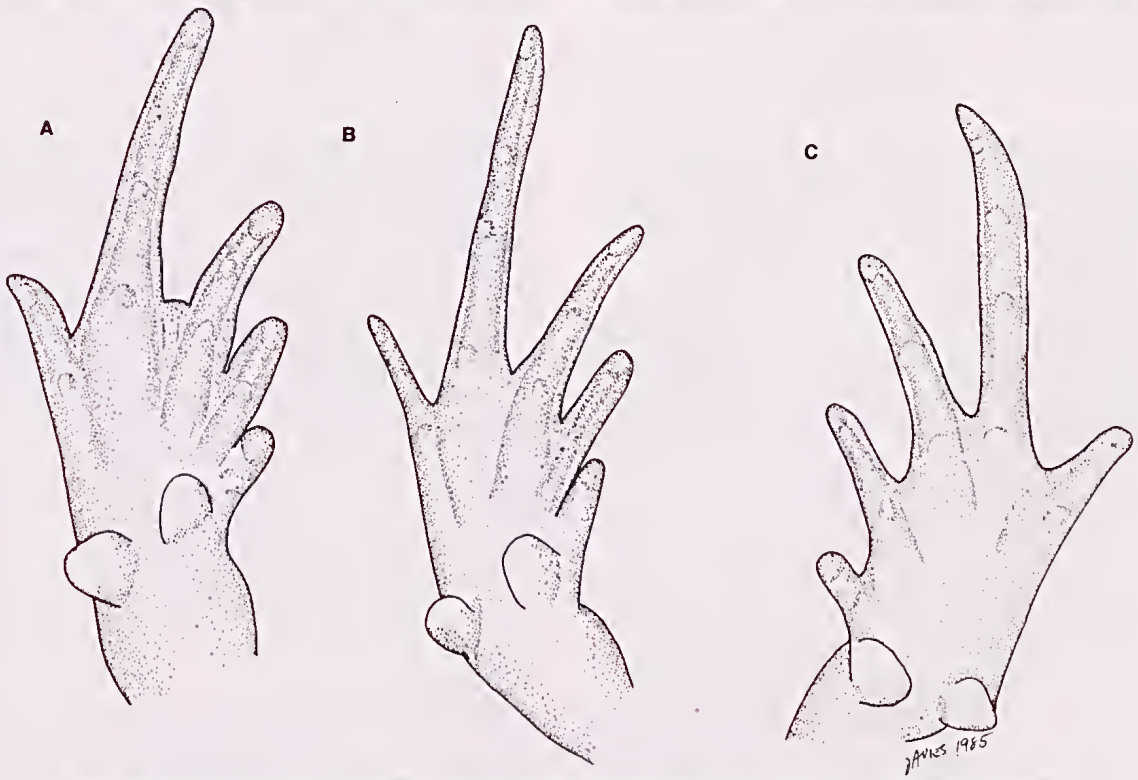

Fig. 4—Variation in the toe webbing and toe fringing in *Uperoleia lithomoda*. A, basal webbing, well fringed, Amber Station, Qld. B, unwebbed, moderate fringing, Gibb River Station, W.A. C, unwebbed, unfringed, Mary River, N.T.

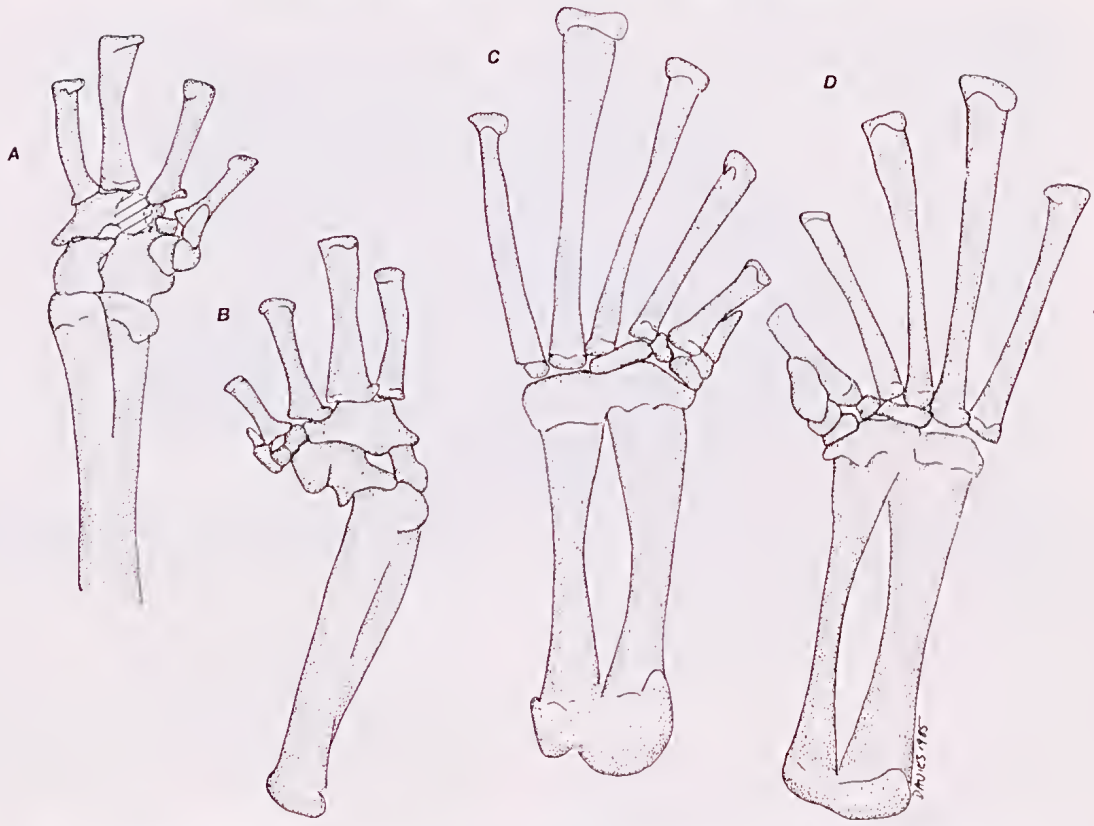

Fig. 5—*Uperoleia lithomoda*, Gibb River, W.A. A, Ventral and B, Dorsal views of carpus. C, Dorsal and D, Ventral views of tarsus.

from Townsville on Charters Towers Rd; J29884, 96 km from Townsville on Charters Towers Rd; J29483, 1 km S Laura; J29316, 1 km E Laura on Laura-Cooktown Rd; SAM R29696, Pajingo Station; R29697, Battery Station; J38545, J38856, J38842, J38844, Pentland, N side of town.

The osteological description of *U. lithomoda* by Tyler *et al.* (1981a) did not include elements of the carpus, tarsus, pelvic girdle or hyoid. These features have proved useful as species characters (Davies & Littlejohn 1986), and we here supplement the original description.

Carpus: The carpus consists of six elements. Quite considerable torsion occurs. Both the O. ulnare and O. radiale are present. The O. radiale is the larger. These elements articulate with the O. radioulna proximally, and with each other on their proximo-medial border. Distally both elements articulate with the large transversely-elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale. The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. From the lateroproximal corner a small, subacuminate flange extends proximally. Ventromedially a palmar sesamoid occurs (Fig. 5). The O. centrale preaxiale articulates laterally with the O. radiale and distally with the O. centrale postaxiale, and with the carpal element of the O. distale carpale 2 (Fig. 5), and laterally with the basal prepollical element. The carpal element of the O. distale carpale 2 articulates with, but is not fused to, the carpal element of the O. distale carpale 3.

Tarsus: The O. tibiale and O. fibulare are elongated elements fused proximally and distally. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III (Fig. 5). It extends laterally to articulate with the medioproximal side of the base of O. metatarsus II. The second element lies at the base and slightly laterally to O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal element of the prehallux is large and extends approximately one half the length of O. metatarsus I (Fig. 5).

Ilium: No ilial crest is developed. The dorsal prominence is wedge-shaped and extremely prominent (Fig. 6). The dorsal protuberance is prominent and posterolateral.

Hyoid: The hyoid plate is approximately as wide as it is long. The alary processes are prominent but not pedunculate. The anteromedial processes of the anterior hyale are short and slender. The posterolateral processes of the hyoid plate are moderately broad and moderately long. The posterior cornua are ossified (Fig. 6).

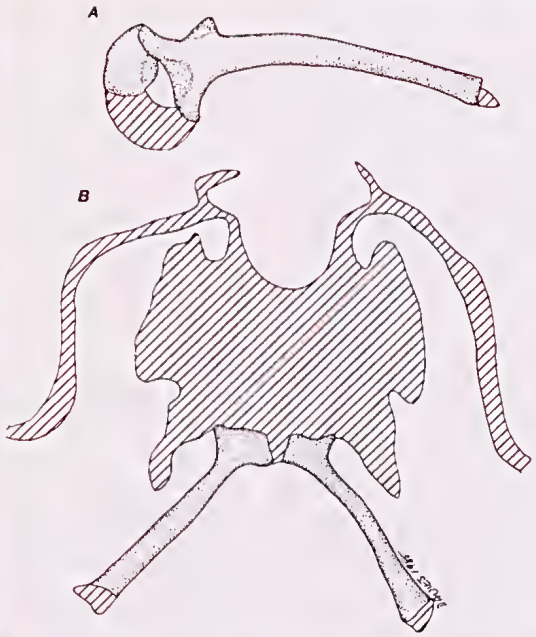

Fig. 6 — *Uperoleia lithomoda* (UAZ B896). A, Lateral view of ilium and B, Ventral view of hyoid.

VARIATION: Skulls of *U. lithomoda* share a combination of features: nasals that are closely-applied anteromedially and widely-separated posteromedially with a crescentic anteromedial edge, and frontoparietals that curve anteromedially on their orbital edges (Fig. 7). Exposure of the frontoparietal fontanelle varies from almost completely roofed with posteromedial fusion of the frontoparietal elements (Fig. 7C) to moderately-widely exposed in young specimens (Fig. 7A). The more common condition is a poorly-exposed frontoparietal fontanelle as shown in Fig. 7B. Approximately one half of the specimens examined had state B, one third had a condition between states B and C and the remainder, state C.

The otic ramus of the squamosal has two conditions; it is short (Fig. 7B) or moderately long (Fig. 7C). The zygomatic ramus of the squamosal is short in all specimens and does not vary. The prootic and exoccipital are never fused (although calcification is common) and ossification of the exoccipitals dorsomedially and ventromedially is always absent. The carotid canal groove is rarely apparent (4 specimens in 48). The palatal shelf is invariably deep. The palatine processes of the premaxillaries are either short and broad or moderately long and slightly more slender. Separation of these elements varies; those exhibiting the short and broad condition tend to be more closely applied than the others. The pterygoid process of the palatal shelf is moderately well developed in all cases.

The palatines are slender and slightly overlap the anterior extremities of the sphenethmoid in ventral view. They are reduced laterally, and do not extend beyond the lateral extremities of the maxillary processes of the nasals. They are slightly expanded medially in many cases and usually angled fairly acutely to the sphenethmoid at an angle approaching 45°; more rarely the angle is slightly flatter.

The cultriform process of the parasphenoid is only moderately broad either reaching the level of the medial extremities of the palatines or not so far. The anterior extremities are slightly serrate, but truneate. The alae of the parasphenoid are at right angles in all but one specimen from Groote Eylandt (the exception is angled slightly posterolaterally). The alae are moderately short, not reaching the extremities of the medial rami of the pterygoids.

The pterygoids are robust. The anterior rami are moderately slender and in moderately long contact with the pterygoid process of the palatal shelf of the maxillaries. The posterior ramus is short, moderately broad and moderately acute. The medial ramus is moderately long (occasionally longer), acuminate, and not in bony contact with the prootic region.

The pars facialis of the maxillary is shallow with a very well-developed preorbital process. The alary processes of the premaxillaries are perpendicular to the pars dentalis, moderately broad at the base and usually bifid dorsally.

Vomerine remnants are absent in all the material examined and invariably a bony columella is present.

HABITAT: *U. lithomoda* calls at the base of grass tussocks usually on coarse gravelly soil at some distance from ephemeral water (Tyler, Watson & Davies unpubl.). If two or more species are calling at the same

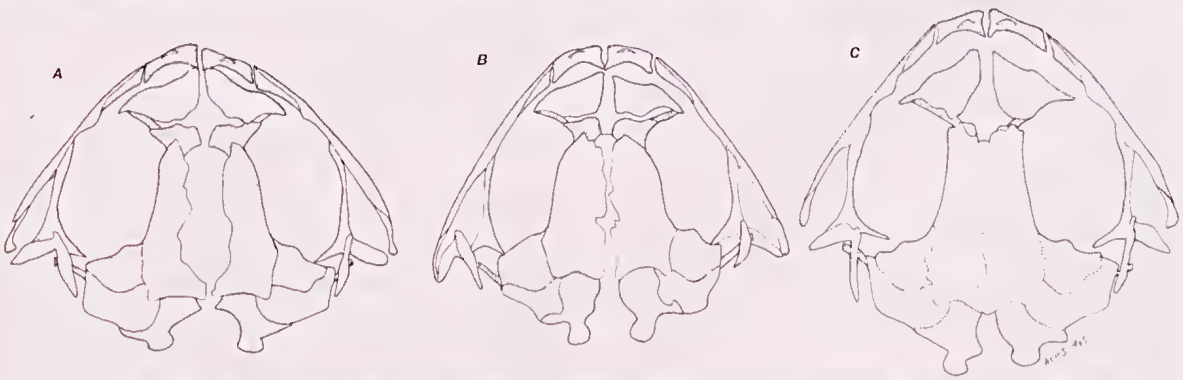

Fig. 7 — Dorsal views of skulls of *Uperoleia lithomoda*. A, C, from Gibb River, W.A. B, from Coen, Qld.

site, the other species (e.g. *U. inundata* on Groote Eylandt and *U. borealis* at Granite Creek in W.A.) calls closer to the water than *U. lithomoda*. Spatial separation is extreme in these situations (Tyler *et al.* 1986). However, at Lakefield (Cape York), *U. lithomoda* and *U. mimula* called at the base of tussocks on inundated floodplain and no spatial separation was apparent. Habitat here included *Melaleuca* woodland, eucalypt woodland, open woodland and eucalypt forest with tussock or sod grassland understorey.

ADVERTISEMENT CALL: Advertisement calls of *U. lithomoda* were described and analysed by Tyler *et al.* (1981a,c). The call is an explosive click that is painful to the ears, in a large chorus. We have examined calls from across the range of *U. lithomoda* in Queensland and find little variability (Table 3). Tyler *et al.* (in press) found the population at Gibb River Station to have fewer pulses per note than those from Lake Argyle and Katherine (which are similar to the Queensland calls analysed here). The result is a considerable lowering of pulse repetition rate (62.5-234.7 pulses sec^{-1} compared with 150-462). This was interpreted as a continuation of an east west trend (substantiated by the data here). Because of the overall similarity of calls of this population with others, the conspecificity of the material was accepted.

DEVELOPMENTAL BIOLOGY: Tadpoles are dark brown on the dorsal and lateral surfaces. The body is flattened dorsally (Fig. 8) with dorsally-located nostrils. The spiracle is sinistral and the vent dextral. The fin is pigmented with islands of fine pigment, the tail tip being black (Fig. 8). The myotomes are mottled with pigment.

The mouth disc is very small. The tooth formula is ⅔ with the lower of the upper rows divided (Fig. 8). The horny beak is weakly developed. A very poorly-developed border of papillae, widely separated anteriorly and posteriorly, surrounds the oral disc.

DISTRIBUTION: *Uperoleia lithomoda* occurs in the Kimberley Division of Western Australia, in the north of the Northern Territory, on Groote Eylandt, at the base of the Gulf of Carpentaria, and on the Cape York Peninsula. Tyler and Davies (1984) reported the species to occur in New Guinea, but this record is not sustained in view of the information now available on the second species known to occur on Cape York. This cryptic species is described on p. 178 and is morphologically very similar to *U. lithomoda*. The distribution of *U. lithomoda* is shown in Fig. 9.

TABLE 3
ADVERTISEMENT CALL CHARACTERISTICS OF THREE SPECIES OF *Uperoleia*.

Species & Locality	N	No. of pulses msec	Duration	Pulse repetition rate (pulses sec^{-1})	Dominant Frequency Hz	Wet bulb temperature °C
Uperoleia lithomoda J.C.U. experimental farm nr Charters Towers (SAM R28870, formerly NPWS N15592)	1	3	13 (10-15)	260 (200-300)	2367 (2300-2400)	24.6°
U. lithomoda Amber Station (SAM R28769, formerly NPWS N28751)	1	3.67 (3-4)	19.3 (18-20)	174 (150-222)	2500	–
U. lithomoda Lakefield (SAM R28771, formerly NPWS N28872)	1	3	11.8 (10-15)	250 (200-300)	3320 (3300-3400)	25.2°
U. lithomoda Coen Airport (UAZ A897, formerly NPWS N32319)	1	3.2 (3-4)	12.2 (10-16)	265 (231-300)	2520 (2500-2600)	24.8°
U. lithomoda 9.6 km N Coen (SAM R29772, formerly NPWS N32388)	1	5.5 (5-6)	21 (20-22)	261 (250-272)	2750 (2700-2800)	24.6°
Uperoleia fusca Type locality (SAM R29596, R29599-29602)	5	20.6 (18-24)	302.1 (220-360)	68.41 (64.86-73.08)	2700	21.5°-23.1°
Uperoleia mimula Townsville Town Common (SAM R29631, R29634-5)	3	4.1 (3-5)	65.5 (55-90)	64.1 (56-83)	2900 (2600-3300)	23.4°-24.0°
U. mimula Lannercost, S.F. (SAM R29627, formerly NPWS N15605)	1	4.7 (4-5)	64 (50-70)	73.5 (71-80)	2750 (2700-2800)	24.8°
U. mimula Bazant Outstation (QM J45943)	1	4.3 (4-5)	43 (40-50)	100 (100)	2800 2800	27.2°

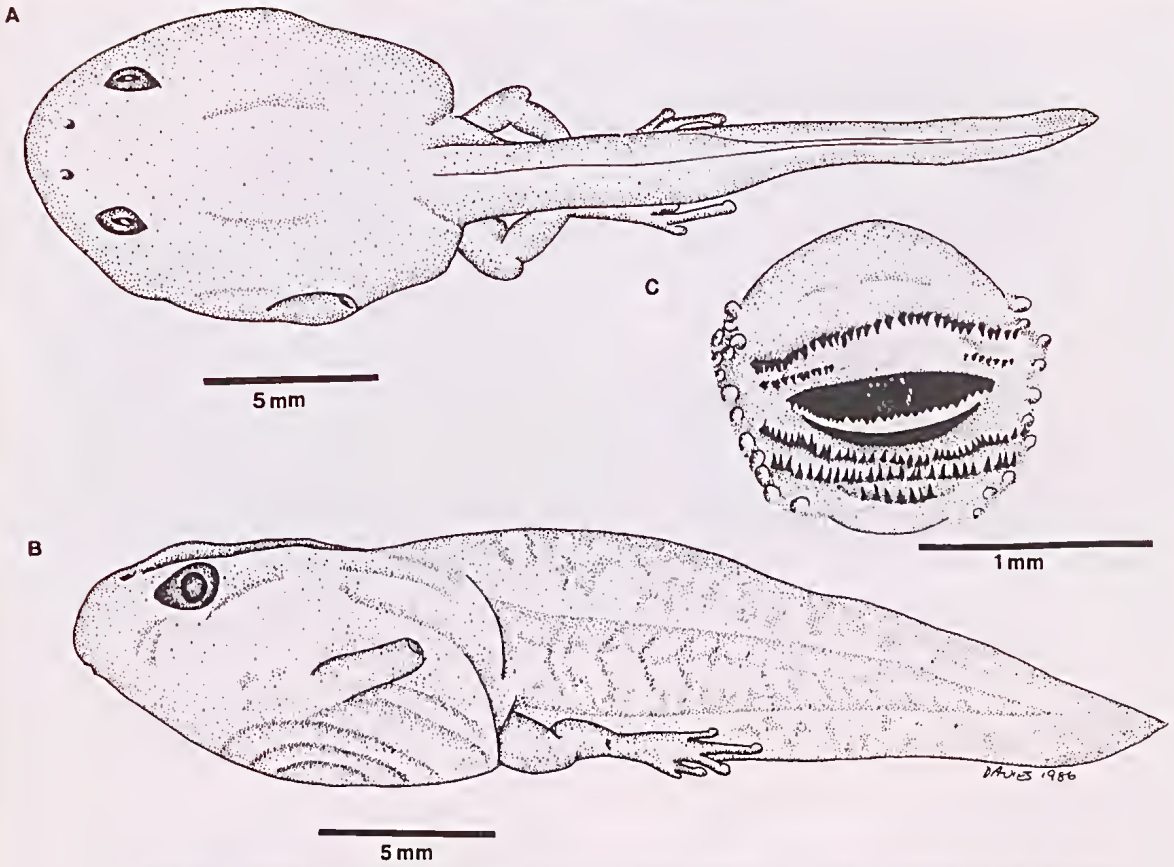

Fig. 8—*Uperoleia lithomoda* tadpole, stage 40 of Gosner (1960), from Newry Station, N.T. A, Dorsal and B, lateral views. C, oral disc.

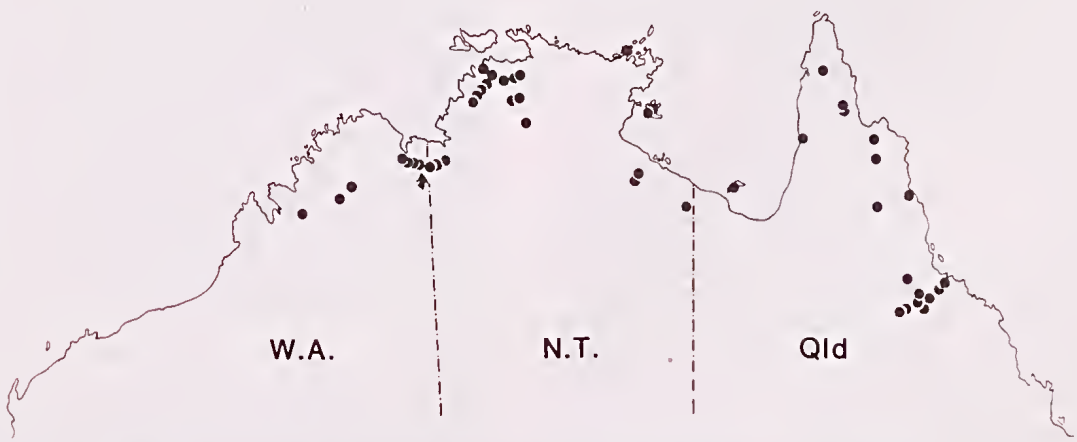

Fig. 9—Distribution of *Uperoleia lithomoda*. The arrow indicates the type locality.

Comparison with Other Species: *Uperoleia lithomoda* is a small to moderately large species (males 19-26 mm, females 17-30 mm) lacking maxillary teeth and with a poorly- to moderately-exposed frontoparietal fontanelle. These features are shared by *U. aspera, U. rugosa, U. mimula* and *U. capitulata.*

From *U. aspera, U. rugosa* and *U. capitulata, U. lithomoda* can be distinguished by a combination of lyrate scapula plicae, gold-tipped parotoid and inguinal glands giving the impression of yellow to cream lateral stripes on the dorsum, and by a very short call consisting of 4-6 rapid pulses.

U. lithomoda is most closely related to *U. mimula.* From this species *U. lithomoda* can be distinguished by the presence of prominent markings on the dorsum, by the lack of ventral pigmentation, by strong development of lateral golden, yellow gold or cream stripes on the dorsum (sometimes developed in *U. mimula*) and by call. (The pulses of the calls of *U. lithomoda* are difficult to delineate whereas those of *U. mimula* are recognisable to the ear—see Fig. 33).

Uperoleia inundata Tyler, Davies and Martin

Pseudophryne fimbrianus?: Parker 1926, p. 670 (part.)
Glauertia orientalis: Parker 1940, p. 67 (part.) Mitchell 1955, p. 404.
Uperoleia orientalis: Tyler, Davies & Martin 1981a, p. 24 (part.)
Uperoleia inundata: Tyler, Davies & Martin 1981, Aust. J. Zool. Suppl. Ser. 79, p. 39.
Uperoleia sp.: Gow, 1981, p. 66.
Uperoleia inundata: Daugherty & Maxson 1982, p. 342; Tyler, Crook & Davies 1983, p. 435; Cogger 1983, p. 83; Cogger, Cameron & Cogger 1983, p. 32; Tyler & Miller 1985, p. 45; Tyler 1985, p. 407; Maxson & Roberts 1985, p. 293; Tyler & Davies 1986, p. 58; Tyler, Davies & Watson 1986, p. 97; Mahony & Robinson, 1986, p. 120.

Definition: A small to moderate-sized species (males 18-29 mm S-V, females 22-32 mm S-V) lacking maxillary teeth; toe webbing basal or absent; parotoid glands prominent; inguinal glands prominent and restricted to inguinal region; frontoparietal fontanelle widely exposed; carpus of six elements; anteromedial processes of anterior hyale of hyoid small and slender; ilial crest absent; dorsum generally smooth; call a short rasp with a pulse repetition rate of 68-163 pulses sec^{-1}.

Material Examined: N.T.: SAM R28645-82, UAZ A829-36, B851-7, 1 km NE Jabiru East Watertank; SAM R28683-28712, UAZ A837-44, B858-61, swamp, 0.4 km from Jabiru East turnoff, Arnhem Hwy; SAM R28713, road to Radon Springs, foot Mt Brockman; SAM R28740, UAZ A596, Chickenhawk Dreaming, 2 km S Cannon Hill; SAM R28716-29, road from Retention Ponds 1 and 2, Jabiru; SAM R28730-33, UAZ A845-8, Retention Pond no. 4, Jabiru; SAM R28734-39, 8 km W Mary River on Arnhem Hwy; SAM R28714-5, 1 km NE Jabiru East turnoff Arnhem Hwy; NTM R12066, Scruttons Lagoon; AMNH 117726, CAS 156682-3, BMNH 1984.9-10, MCZ A106702, NTM R12527, R12532-44, SAM R25539-44, 8.2 km N Emerald River, Groote Eylandt; AM R112420, NTM R12529, 18.3 km E Angurugu Airport, Groote Eylandt; AM R11249, KU 196728, NTM R12530, 5.6 km E Angurugu Airport, Groote Eylandt; KU 196729, NTM R12531, SAM R25545, Amagula Pools, Groote Eylandt; AM R53299-303, Caranbirini W.H., approx. 21 km from McArthur River (16°18′, 136°05′); AM R53351, R53353, 36.5 km N McArthur River Camp on Borroloola Rd (16°06′, 136°07′); AM R53506, R53616-18, R53621, R53736-8, 15 km N McArthur River Camp on Borroloola Rd (16°15′, 136°04′); AM R53691-2, 10 km N McArthur River Camp on Borroloola Rd; SAM R12741-74, R14186, Fish River Gorge; SAM R12743, R13864, 15.4 km S Hayes Creek.

Qld: NTM R12070, Westmoreland.

External Morphology: Specimens of *U. inundata* from mainland Australia are smaller than those on Groote Eylandt (Tyler *et al.* 1986). The largest males examined from the mainland are 26 mm S-V and females 27 mm S-V compared with 29 mm S-V for males and 32 mm S-V for females on Groote Eylandt. Apart from size, the species is morphologically conservative. The snout is relatively narrow [E-N/1N $1.41 \pm .21$, (0.93-2.00)] and in Groote Eylandt specimens and some mainland specimens it protrudes beyond the lower jaw (Fig. 10). Approximately equal numbers of specimens have rounded or truncate snouts when viewed from above.

The hind limbs are short [TL/S-V $0.34 \pm .02$, (0.30-0.37)] and on Groote Eylandt specimens are even shorter ($0.32 \pm .02$, Tyler *et al.* 1986).

The fingers are very rarely fringed. Subarticular tubercles are moderately prominent (Fig. 11). Palmar tubercles are very poorly developed, particularly that at the base of the thumb. This is scarcely detectable in males as it is masked by the unpigmented glandular nuptial pad.

Fringing on the toes is poor in most of the specimens examined but moderately to well-fringed in the rest. Toe fringing is absent in Jabiru material but present in southern Gulf of Carpentaria material. Toe webbing is absent in about one quarter of the specimens examined and basal in the remainder. About one-third of this basally-webbed material exhibits a slightly tubercular nature in this basal webbing (Fig. 11). Subarticular tubercles are conical. The inner metatarsal tubercle is oriented along the axis of the first toe and the outer metatarsal tubercle is angled to the long axis of the foot. The metatarsal tubercles are particularly large in Groote Eylandt and southern Gulf of Carpentaria material, but smaller and slightly compressed in much of the Jabiru material, giving the appearance of possible abrasion and wear.

The dorsum is smooth in most of the specimens examined and mildly tubercular in the remainder. The parotoid glands are prominent in all specimens and usually are cream. Inguinal glands are always prominent and always truly inguinal, being discreet and never extending anteriorly along the flanks. Coccygeal glands are usually very pro-

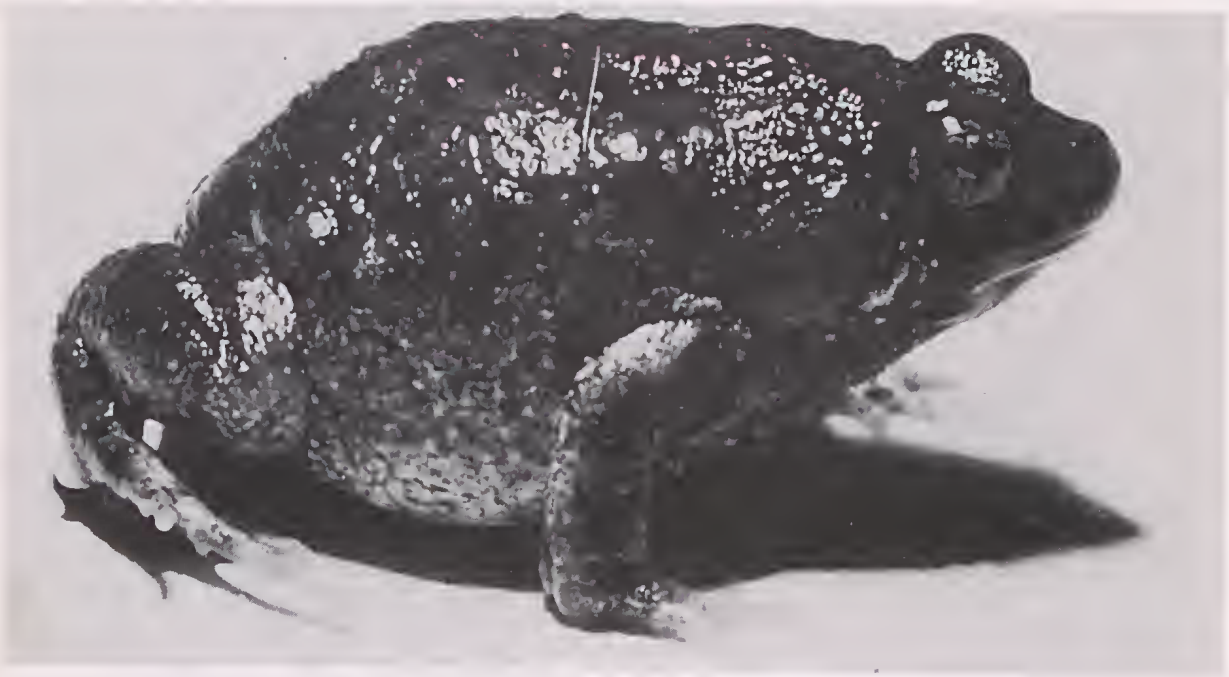

Fig. 10 – *Uperoleia inundata* in life (Groote Eylandt).

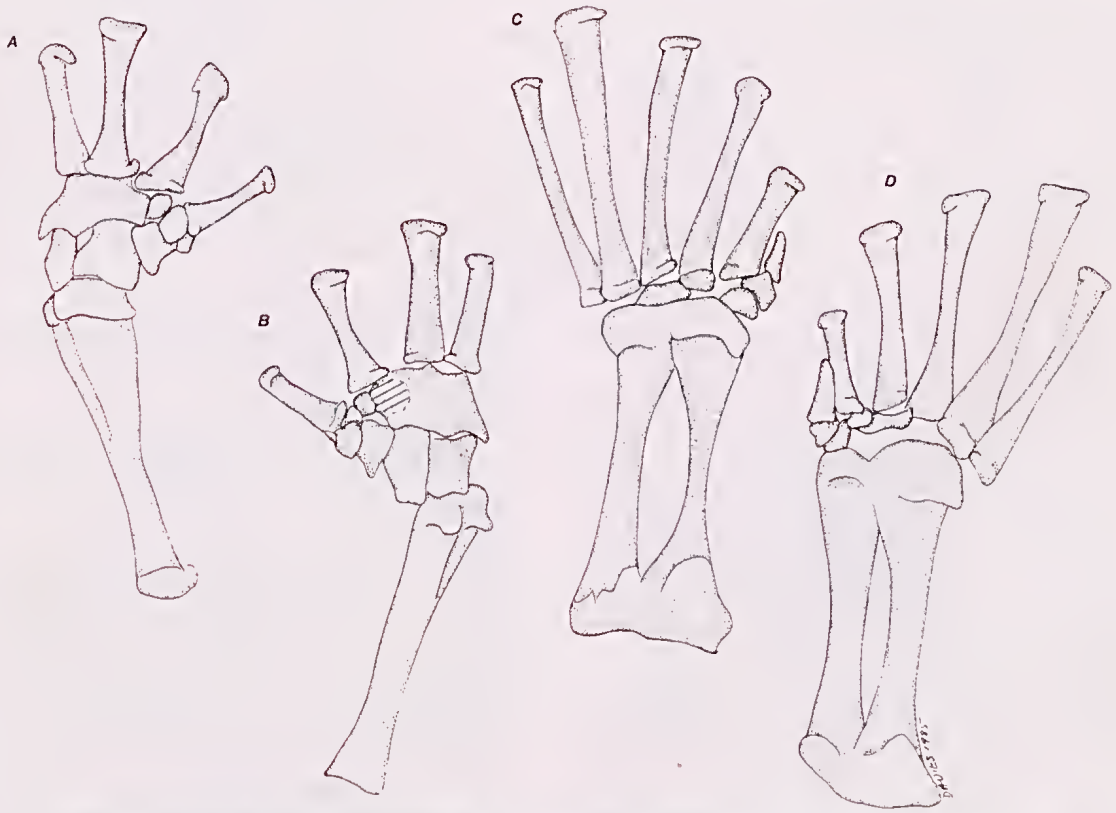

Fig. 12 – *Uperoleia inundata* (UAZ A397). A, Dorsal and B, Ventral views of carpus. C, Dorsal and D, Ventral views of tarsus.

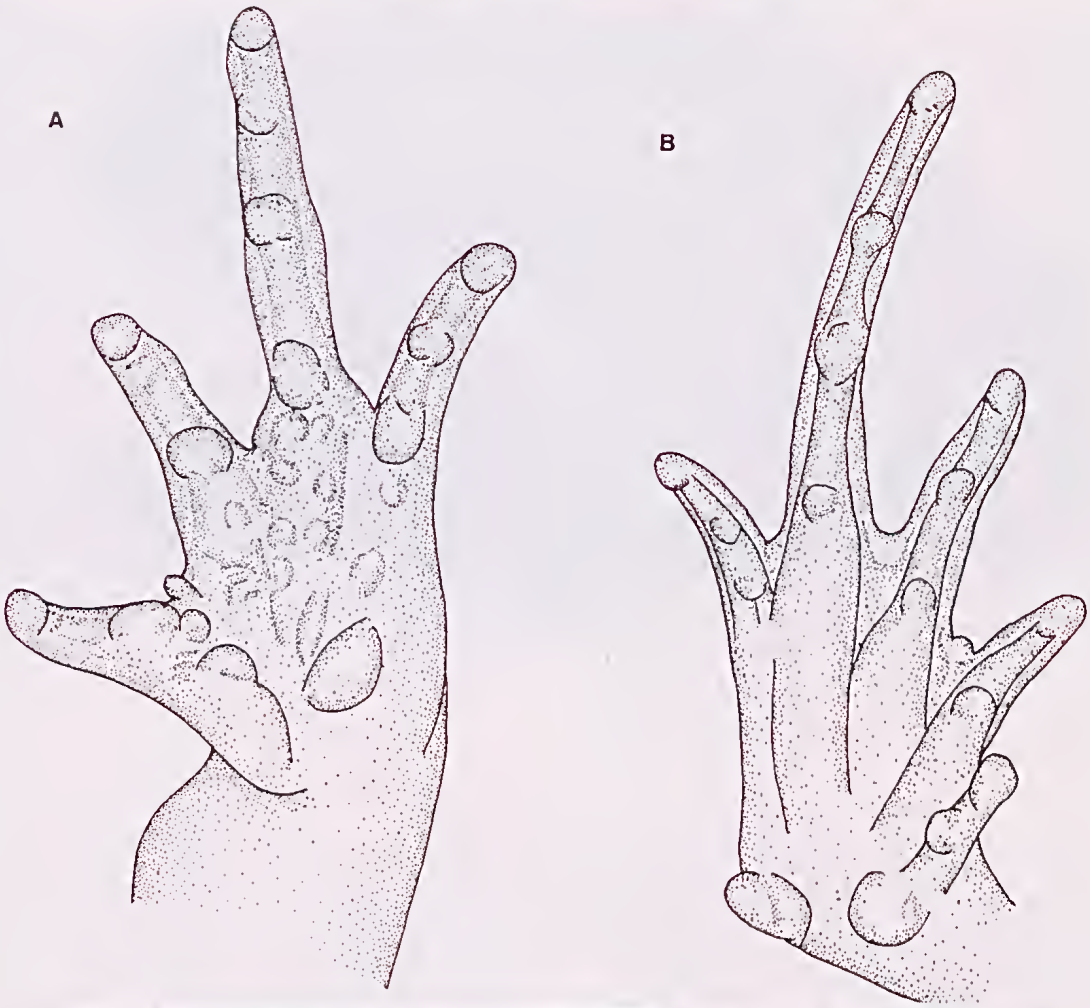

Fig. 11—*Uperoleia inundata* (Groote Eylandt) (NTM R12529). A, Palmar view of hand. B, Plantar view of foot.

minent. The submandibular gland is discreet or disrupted in approximately equal proportions.

Scapular plicae are absent. Anterior eyeflaps are very poorly developed and cloacal flaps are poorly fimbriated. The ventral surface is granular in most of the specimens but is occasionally smooth. Dorsal patterning is very indistinct in most material; when present it is in the form of blotches of pigment with no strong outline.

Ventral pigmentation is absent in about two thirds of the specimens and faint in the remainder. Groote Eylandt material is slightly more ventrally pigmented than mainland material.

Inguinal and femoral patches are not prominent.

Osteology: *Material examined*: N.T.: UAZ A818-826, 100 m E Jim Jim Turnoff, Arnhem Hwy; UAZ A827, Jabiru East Airstrip; UAZ A829-36, B851-57, Western end Jabiru East Airstrip; UAZ A837-44, B858-61, swamp, 0.4 km S Jabiru East turnoff; UAZ A845-48, Retention Pond no. 4; AUZ A849-50, Daly River Rd; UAZ A596, Chickenhawk Dreaming, 2 km S Cannon Hill; UAZ A395(2), SAM R17268, Fish River Gorge; UAZ B397, B479, Darwin; UAZ A898, SAM R25540-41, Groote Eylandt.

The osteological description of *U. inundata* of Tyler *et al.* (1981a) did not include elements of the carpus, tarsus, pelvic girdle and hyoid. Here we supplement the original description.

Carpus: The carpus consists of six elements. Quite considerable torsion occurs. Both the O. ulnare and O. radiale are present; the O. radiale is the larger. These elements articulate with the O. radioulna proximally and with each other on their proximo-medial borders. Distally, both elements articulate with the large, transversely-elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale. The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. From the lateroproximal corner, a small flange extends proximally. Anteroventrally a palmar sesamoid is located. The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and

with the carpal elements of the O. distale carpale 2 and 3 and laterally with the basal prepollical element (Fig. 12).

Tarsus: The O. tibiale and O. fibulare are elongated elements fused together at either end. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest, and lies at the base of O. metatarsus III. It extends laterally to articulate with the medioproximal side of the base of O. metatarsus IV and medially to the base of O. metatarsus II. The second element lies at the base of O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is moderately broad and elongate, extending for approximately half the length of O. metatarsus I (Fig. 12).

Pelvic Girdle: No ilial crest is present. The dorsal prominence is small, gently monticuline, with a dorsolateral protuberance (Fig. 13). The pubis is calcified.

Hyoid: The hyoid plate is longer than wide. The antero-medial processes of the anterior hyale are small and slender. The alary processes of the hyoid plate are not pedunculate. The posterolateral processes are slender and moderately long. The posterior cornua are ossified (Fig. 13).

VARIATION: The nasals are only moderately ossified, widely-separated posteromedially and with characteristic indentations and crenulations on the posterior edge (Fig. 14). Lack of ossification giving indentations on posterior edges is common in *U. inundata*. The nasals are very occasionally crescentic on their anteromedial edges.

The frontoparietal elements characteristically extend anterolaterally to the poorly-ossified sphenethmoid. In most specimens the orbital edges are very straight and perpendicular to the prootic. In a few specimens they are inclined slightly medially (Fig. 14). The frontoparietal fontanelle is usually very widely exposed, sometimes slightly less so. Exposure is usually greater than shown in Fig. 14.

The exoccipital and prootic are never fused and dorsomedial and ventromedial ossification of the exoccipital is lacking. The crista parotica is always short and stocky and the epiotic eminences are prominent.

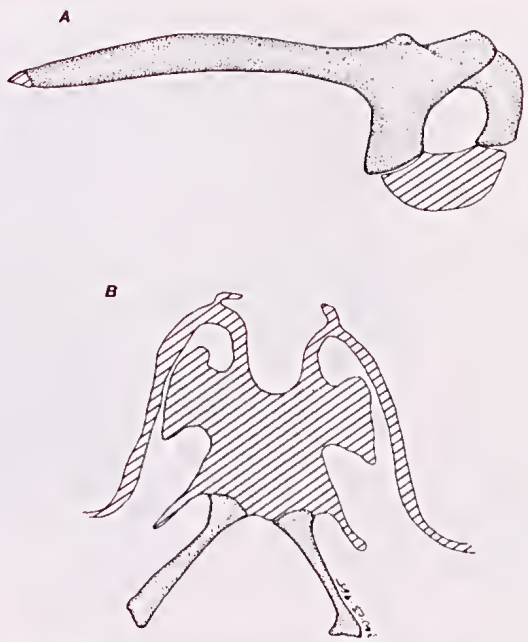

Fig. 13—*Uperoleia inundata* (UAZ B479). A, Lateral view of ilium. B, ventral view of hyoid.

The condition of the zygomatic ramus of the squamosal varies. It is absent, tiny and straight, or tiny and knobbed. The otic ramus varies slightly in length: the usual condition is moderately long.

The palatines are expanded medially in about two-thirds of the specimens and unexpanded in the remainder. The cultriform process of the parasphenoid invariably is long and usually truncate. The alae are at right angles to the cultriform process; they are slender to moderately slender and vary slightly in length (Fig. 14).

The medial ramus of the pterygoid is usually very long and acuminate. Occasionally it is shorter and

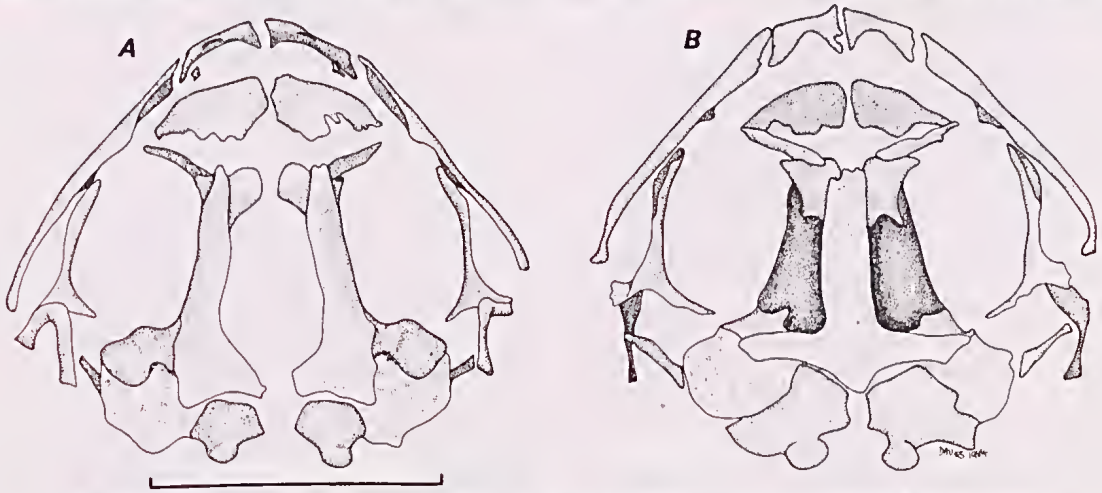

Fig. 14—*Uperoleia inundata* (SAM R25541). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

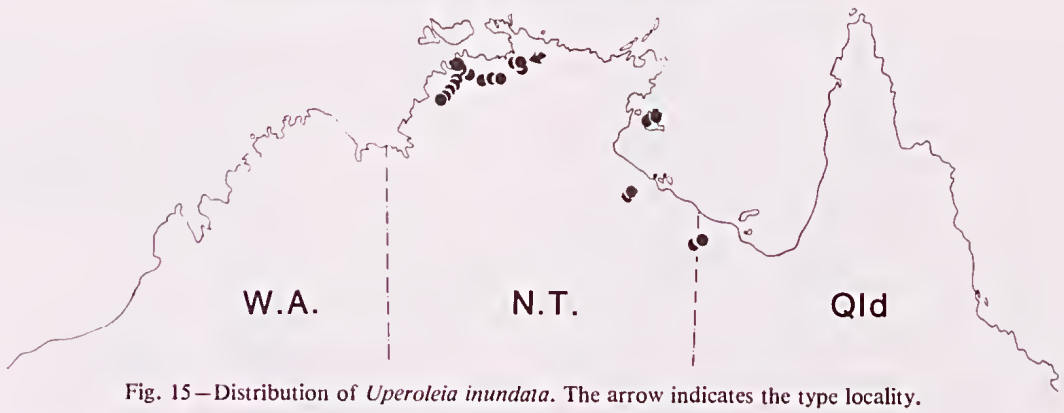

Fig. 15—Distribution of *Uperoleia inundata*. The arrow indicates the type locality.

acuminate. The posterior process is usually broad, occasionally moderately acuminate. The anterior ramus is always in long contact with the maxillary.

The pars facialis of the maxillary varies slightly in depth. It is rarely shallow, and is usually moderately deep. The preorbital process is present, and usually well developed but can vary slightly in prominence.

The alary proeesses of the premaxillaries are inclined anteromedially. In one specimen (SAM R17268), they are unusually high. The palatine processes of the premaxillaries are usually moderately long and not closely applied; rarely, they are short.

The pterygoid process of the palatal shelf is usually poorly to moderately developed. Very rarely it is virtually absent (Fig. 14).

HABITAT: Males eall from shallow water at the base of grass tussocks, under leaves and logs, from grass stems in water, and under leaf litter in sandy stream beds (Tyler *et al.* 1983, Tyler *et al.* 1986).

ADVERTISEMENT CALL: The call of *U. inundata* is a 'long call' of extreme variability. At least two calls are produced (Tyler *et al.* 1981a, Tyler *et al.* 1986).

LIFE HISTORY: Tyler *et al.* (1983) described the life history of this speeies and illustrated larval morphology ineluding mouth disc structure.

DISTRIBUTION: *Uperoleia inundata* oeeurs in the north of the Northern Territory, on Groote Eylandt and on the western and southern coasts of the Gulf of Carpentaria. It penetrates into Queensland at the base of the Gulf of Carpentaria (collected at Westmoreland) (Fig. 15).

COMPARISON WITH OTHER SPECIES: *Uperoleia inundata* is an untoothed species with a widely-exposed frontoparietal fontanelle, features shared by *U. russelli, U. glandulosa, U. talpa, U. orientalis, U. crassa, U. borealis, U. arenicola* and *U. littlejohni*.

U. inundata may be distinguished from *U. russelli, U. crassa, U. talpa, U. orientalis* and *U. borealis* by poor toe webbing (absent or basal).

From *U. glandulosa* and *U. littlejohni, U. inundata* is distinguished by the absence of broad toe fringing and by the lack of strong dorsal patterning.

From *U. arenicola, U. inundata* is distinguished by greater ossification of the nasals.

Uperoleia trachyderma Tyler, Davies and Martin

Uperoleia trachyderma Tyler, Davies & Martin 1981, Trans. R. Soc. S. Aust. 105, p. 149.

Uperoleia trachyderma: Tyler, Davies & Martin 1983, p. 241; Cogger 1983, p. 87; Cogger, Cameron & Cogger 1983, p. 34; Tyler & Miller 1985, p. 45; Tyler 1985, p. 409; Tyler & Davies 1986, p. 60.

DEFINITION: A small to moderate-sized species (males 17-26 mm S-V) lacking maxillary teeth, with small eyes; toes broadly fringed; very small, rounded, outer metatarsal tubercle; widely-exposed frontoparietal fontanelle; dorsum covered with small conical tubercles; carpus of five elements; anteromedial processes of anterior hyale of hyoid slender; small ilial crest; call a staceato burst of four short pulses, with a pulse repetition rate of about 79 pulses sec^{-1}.

MATERIAL EXAMINED: N.T.: SAM R22336-48, Rankine River at Ranken Store, Alexandria Station; SAM R22325-35, Barkly Hwy, 500 m N Microwave Repeater 8502 Soudan Outstation, Alexandria Station; SAM R25952-61, 113.9 km S Victoria Hwy/Delamere Hwy Jcn; SAM R24017, 415.1 km W Katherine on Victoria Hwy; SAM R24018-25, 4.4 km W Keep River (Newry Station) on Victoria Hwy.

Qld: QM J39012, Gunpowder Rd, 45.1 km E Mt Isa (20°23', 139°20'); QM J38969-72, J38975, 20 km E Cloncurry on Julia Creek Rd; QM J39089-91, 12.6 km E Camoweal on Barkly Hwy; QM J38965-8, 13.2 km E Cloncurry on Julia Ck Rd; QM J45955, SAM R29660-4, Lawn Hill Station.

EXTERNAL MORPHOLOGY: This species shows little morphological variation and is charaeterised by a finely-tubercular dorsum (Tyler *et al.* 1981c), the texture of which has not been reported in any other Australian amphibian. Only males have been collected; those from western Qld are larger (21-26 mm S-V) than those from localities in the N.T. (17-23 mm S-V).

Hind limbs are moderately long [TL/S-V $0.35 \pm .02$, (0.31-0.39)] and eye to naris distance is always greater than internarial span [E-N/IN $1.35 \pm .16$ (1.07-1.83)]. The eye is consistently small, approximating eye to naris distance in the 56 specimens examined (Fig. 16).

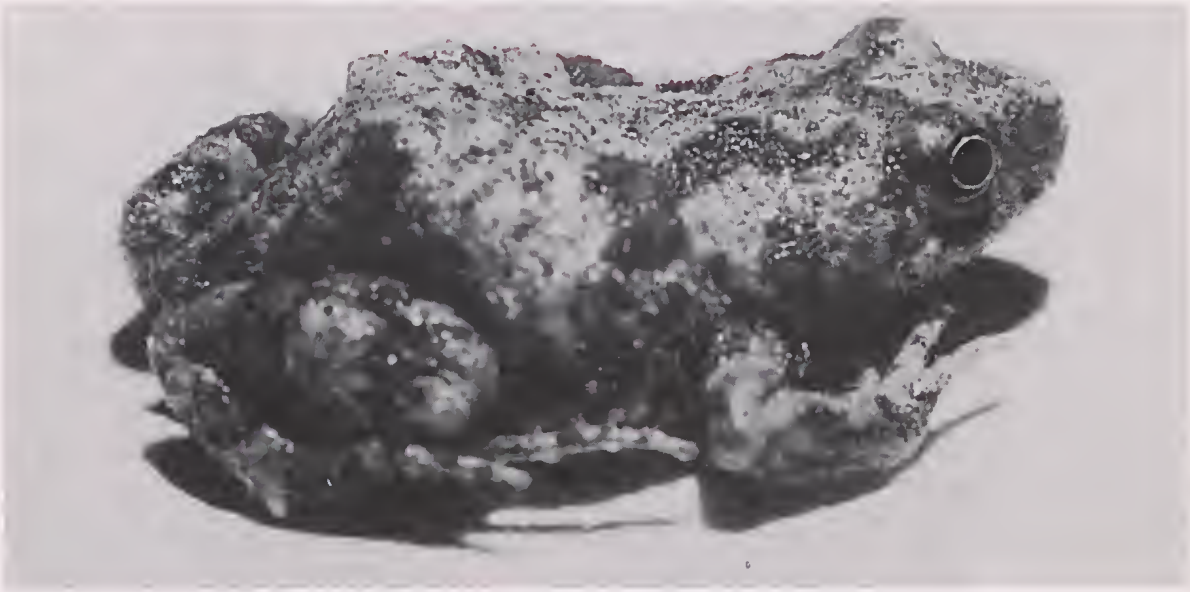

Fig. 16—*Uperoleia trachyderma* in life (Alexandria Station, N.T.).

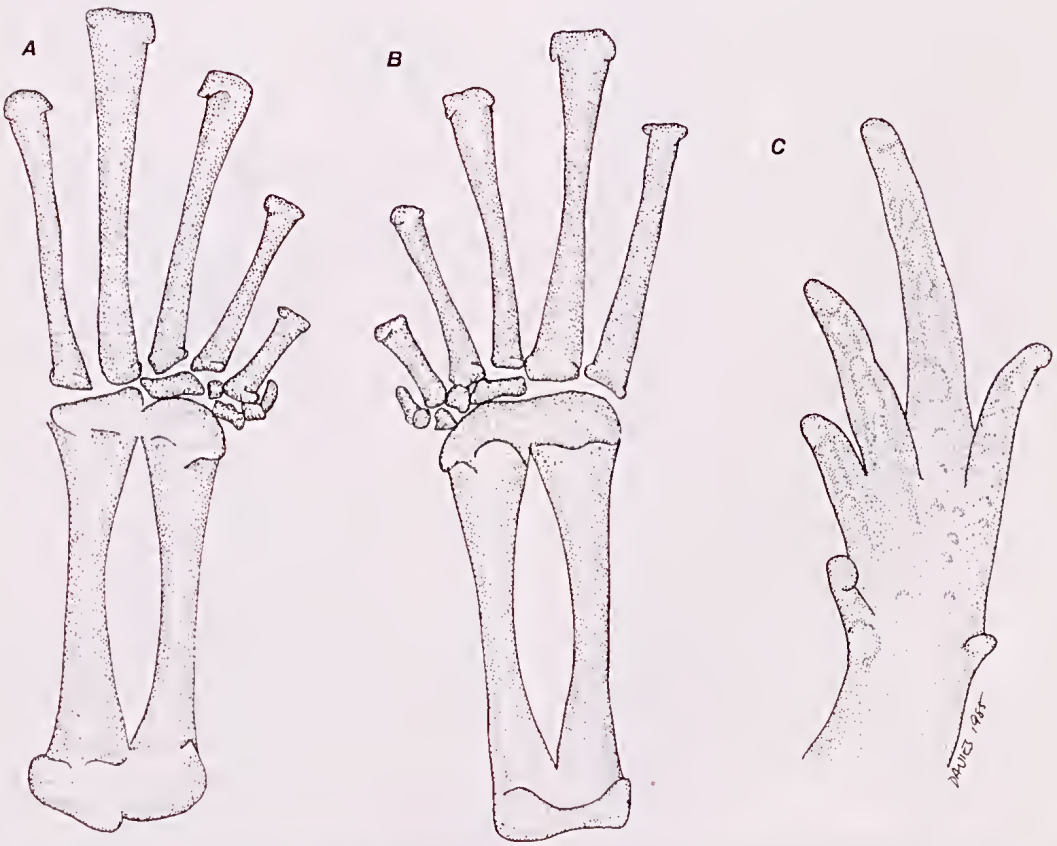

Fig. 17—*Uperoleia trachyderma*. A, Dorsal and B, Ventral view of tarsus (SAM R22331). C, Plantar view of foot (QM J38965).

Toes are well fringed; some specimens are unwebbed whilst others have basal webbing between the toes. Metatarsal tubercles are rounded and small. The inner is situated at the base of toe I and the outer is slightly angled to the long axis of the foot (Fig. 17C).

The characteristic tiny conical tubercles on the dorsal surface (Fig. 16) are restricted occasionally to the head and limbs, with only a trace on the dorsum.

Ventral pigmentation is not always as dense as reported in the type description. Dark stippling is exhibited in only some specimens and most have only a faint suffusion of pigment. In life, the frogs often have brilliant orange patches on the dermal glands (see Tyler & Davies, 1986, p. 50 for a colour illustration of this species) and they have a characteristic posture in which the head is depressed (Fig. 16).

OSTEOLOGY: *Material examined*: N.T.: SAM R22331, UAZ A621, A892-4, Barkly Hwy, 500 km N Microwave Repeater 8502, Soudan Outstation, Alexandria Station; UAZ A622, Rankine River at Ranken Store; UAZ A595-6, 113.9 km S Delamere Hwy/Victoria Hwy Jcn; UAZ A595, 4.4 km W Keep River on Victoria Hwy.

Here we supplement the type description with data on elements of the carpus, tarsus, pelvic girdle and hyoid.

Carpus: The carpus consists of five elements. Little torsion occurs. Both the O. ulnare and O. radiale are present. The O. radiale is the larger of the two. These elements articulate with the O. radioulna proximally and with each other on their proximomedial border. Distally both elements articulate wth the large transversely-elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. preaxiale centrale (Fig. 18). The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. No flange is apparent on the lateroproximal corner of the O. centrale postaxiale. Ventromedially is a depression on which a palmar sesamoid is situated. The O. centrale preaxiale articulates laterally with the O. radiale and distally with the fused carpal elements of the O. distale carpale 2 and 3 and laterally with the basal prepollical element.

Tarsus: The O. tibiale and O. fibulare are elongated elements fused proximally and distally. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III. It extends laterally to articulate with the medioproximal side of the base of O. metatarsus II. The second element lies at the base, slightly laterally, to O. metatarsus II. The medial element lies at the base of O. metatarsus I, and articulates with the O. centrale prehallucis. The distal prehallical element is small and slender (Fig. 17A, B).

Pelvic Girdle: A small proximal crest occurs on the ilium. The dorsal prominence is monticuline and supports a curved posterolateral protuberance (Fig. 19). The pubis is calcified.

Hyoid: The hyoid plate is about as broad as it is long. The alary processes are broad and not pedunculate. The anteromedial processes of the anterior hyale are slender and moderately long. The posterolateral processes of the plate are moderatcly broad and moderately long. The posterior cornua are ossified (Fig. 19).

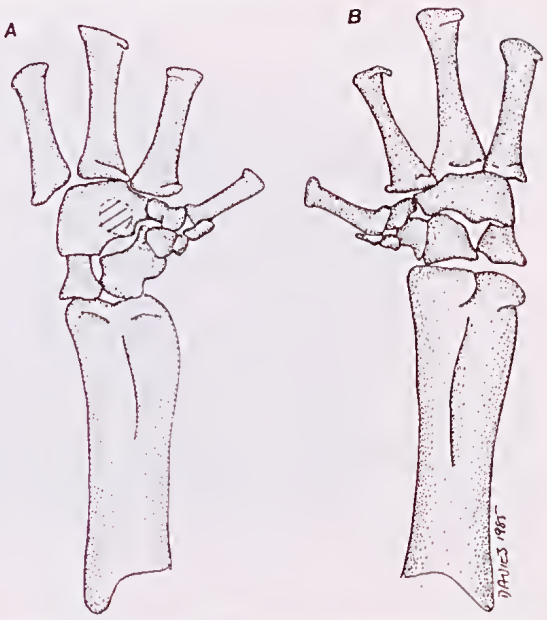

Fig. 18—*Uperoleia trachyderma* (SAM R22331). A, Ventral and B, Dorsal view of carpus.

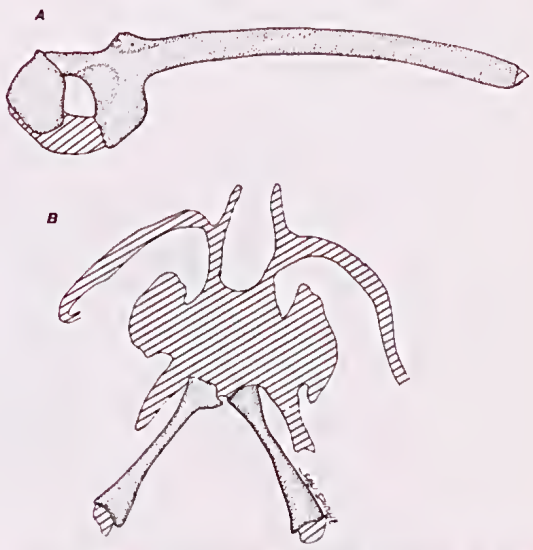

Fig. 19—*Uperoleia trachyderma* (SAM R22331). A, Lateral view of pelvis. B, Ventral view of hyoid.

VARIATION: There is little variation in cranial osteology in the material examined. The nasals are very well ossified with slight variation in the degree of posteromedial separation. The nasals arc always in tenuous contact with the sphcnethmoid. The frontoparietal fontanelle is widely exposed and slight variation occurs in curvature of the orbital edges of the frontoparietal elements. Occasionally curvature is not detectable. The anterior extremitics of the frontoparictals do not reach beyond the sphenethmoid.

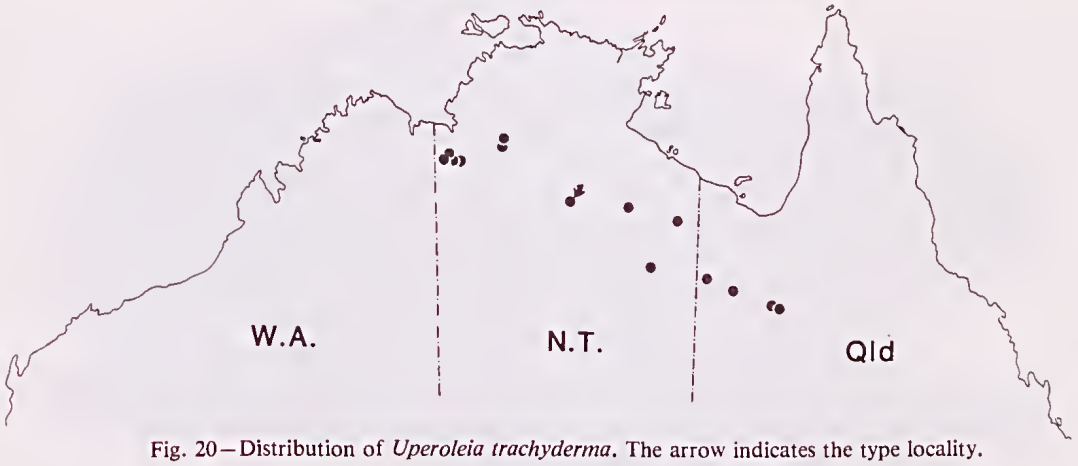

Fig. 20—Distribution of *Uperoleia trachyderma*. The arrow indicates the type locality.

The epiotic eminences are not prominent and posterior ossification appears to be complete, if thin. The zygomatic ramus of the squamosal is small but not bifid and some variation is found in length of the short otic ramus.

The maxillary and premaxillary are edentate and the pars facialis of the maxillary is shallow with a small preorbital process.

The palatines are acutely angled to the sphenethmoid, reduced laterally and do not extend beyond the truncated maxillary processes of the nasals. Vomerine fragments are present medial to the palatines in three specimens.

The anterior ramus of the pterygoid is in moderately-long contact with the moderately-prominent pterygoid process of the palatal shelf of the maxillary.

The cultriform process of the parasphenoid is broad in this species and the alae are short and angled slightly posterolaterally.

The distal carpale 2 and 3 are fused in all specimens.

Advertisement Call: Tyler *et al.* (1981c) reported the advertisement call of *U. trachyderma* from the type locality as a harsh 'creak' of four short pulses with a pulse repetition rate of about 79 pulses sec^{-1}.

Distribution: *Uperoleia trachyderma* is confined to the grey self-mulching cracking clays (Northcote *et al.* 1975) of the Northern Territory and western Queensland (Fig. 20). *U. trachyderma* is the only species within *Uperoleia* that can be associated with a particular soil type (Tyler, Davies, Watson, Martin unpubl., Tyler & Davies 1986).

Comparison with Other Species: *Uperoleia trachyderma* is an untoothed species with a widely-exposed frontoparietal fontanelle, features shared by *U. russelli, U. talpa, U. glandulosa, U. crassa, U. borealis, U. orientalis, U. inundata* and *U. arenicola*.

From *U. russelli, U. talpa, U. crassa, U. borealis, U. glandulosa* and *U. orientalis, U. trachyderma* is distinguished by the absence of webbing or presence of only basal webbing on the toes. From *U. inundata* and *U. arenicola, U. trachyderma* is distinguished by the presence of broad fringes on the toes and a tiny conical outer metatarsal tubercle (broad and elevated in the former two species).

Uperoleia capitulata sp. nov.

Holotype: QM J26428, an adult male collected at Bollon, Queensland (28°02', 147°29') on 22.viii.1975 by G. Czechura.

Definition: A moderate-sized species (males 19-27 mm S-V, females 27-28 mm S-V) with a tiny head; relatively smooth dorsum; hypertrophied dermal glands; maxillary teeth absent; frontoparietal fontanelle poorly exposed; no webbing between the toes; outer metatarsal tubercle rounded and angled moderately acutely to the long axis of the foot; carpus of five elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Call not known.

Description of Holotype: Maxillary teeth absent. Vomerine teeth absent. Snout short, truncated when viewed from above and rounded in profile (Fig. 22). Eye to naris distance greater than internarial span (E-N/IN 1.40). Canthus rostralis inconspicuous and straight. Tympanum not visible externally (Fig. 22). Head small in relation to body (Fig. 22). Fingers long, slender, fringed and unwebbed with prominent subarticular tubercles (Fig. 22). In order of length, 3>4>2>1. Palmar tubercles prominent, that at base of thumb less conspicuous. Hind limbs short (TL/S-V 0.36). Toes long, moderately fringed, unwebbed with conical subarticular tubercles (Fig. 22). Inner and outer metatarsal tubercles prominent, raised; inner gently rounded, aligned along axis of, and encroaching upon, digit 1; outer rounded, angled moderately acutely to axis of foot. Toes in order of length 4>3>5>2>1.

Dorsal surface smooth with hypertrophied parotoid, inguinal and coccygeal glands. Submandibular gland diserete, displaced to anterior face of hypertrophied parotoid gland. Finely-fimbriated supracloaeal flap. Ventral surface smooth.

Male with unilobular submandibular vocal sac. In preservative, dorsal surface grey with darker chocolate markings. Parotoid, inguinal and coccygeal glands with cream markings. Ventral surface cream with faint

Fig. 21 – *Uperoleia capitulata* sp. nov. from Charleville, Qld (SAM R29593).

dusting of patches of chocolate pigment granules. Pale patches in groin and post femoral regions.

Colour in Life (based on SAM R29593): Ground colour grey with well-defined dark grey patches upon the head, scapulae, mid dorsum, and coccygeal region, and narrow transverse bars across the limbs. Faint spectrum orange (Smithe 1975) spots upon the parotoid, inguinal and coccygeal glands and on tips of some small dorsal tubercles. Ventrally whitish with faint brown stipples just behind pectoral region, and on flanks. Throat grey with fine white stipples in male. Pectoral region and ventral thighs unpigmented. Inguinal and femoral patches flame scarlet.

Dimensions (in mm): Snout-vent length 23.8; tibia length 8.5; eye diameter 2.2; eye-naris distance 2.1; internarial span 1.5.

Variation: There are 27 paratypes, 20 ♂♂ 3 ♀♀ and 4 subadults.

Qld: QM J26427, taken with the holotype; J39196, Byanda Station, 20 km WNW Proston, T. Pulsford, 11.i.1981; QM J26416, 1 km N Thargomindah, G. Ingram *et al.*, 24.viii.1975; SAM R29586-7, QM J45960, CAS 160141, 64 km SW Bulloo Downs Hstd, D. G. McGreevy, S. Tickler, 2.x.1976; SAM R29588, QM J45956, Noccundra Hotel, K. R. McDonald, D. G. McGreevy, 30.xi.1975; QM J45957-8, SAM R29590, Boorara Station, 32 km N Hungerford, S. May, late 1976; SAM 29589 Boorara Station, D. G. McGreevy 12.i.1977; SAM R29591, KU 205026, King Tank, Ambathala Nature Reference Site (26°00′, 145°00′), K. R. McDonald, D. G. McGreevy 3.v.1979; SAM R29592-5, QM J45959, DP1 Swamp, Charleville, P. D. McRae, 10.ii.1986.

N.S.W.: AM R24474, R24479, R24481, R24488, R24492, Nyngan, H. G. Cogger, 11.i.1964; AM R28636-7, between Nyngan and Nevertire, W. McCreaddie, 6.xi.1969.

All paratypes are small-headed, robust specimens with bold dorsal patterning of chocolate on a grey and brown background, and cream dermal glands. Males range from 19-27 mm, females 27-28 mm. Hind limbs are relatively long [TL/S-V 0.37 ± .02 (♂♂ 0.34-0.40, ♀♀ 0.31-0.36)]. Eye to naris distance is greater than internarial span [E-N/IN 1.36 ± .25 (1.1-2.08)].

Ventral patterning is better developed in some paratypes, but is never more than patches of brown pigment on the anterior half of the body. The dorsum is faintly or moderately rugose in some specimens (Fig. 21) and hypertrophy of the dermal glands is not always as acute as in the holotype. The snout is sometimes more rounded. Toes rarely show greater fringing than described. The inguinal and post-femoral, light-coloured patches are often more obvious than in the holotype. A pale stripe occasionally occurs in the midline of the head.

Osteology (based on SAM R29586): Skull moderately ossified, sloping anteroventrally. Ossification of sphenethmoid incomplete medially; anterior extremities not extending anteriorly to frontoparietals dorsally; extending about ⅓ posteriorly on length of orbit in ventral view. Prootic not fused with exoccipital. Exoccipital not confluent dorso- or ventromedially. Crista parotica short, stocky, not articulating with otic ramus of squamosal. Very shallow groove of carotid canal on frontoparietals medial to epiotic eminences. Frontoparietal fontanelle poorly exposed, overlain by medially-crenate frontoparietals (Fig. 23) extending entire length of orbit. Anterior margin of fontanelle formed by sphenethmoid at level about ¼ posteriorly on length of orbit. Posterior margin undefined because of absence of medial prootic ossification.

Nasals large, approximately triangular, projecting ventrally at lateral extremities, and with slightly-concave anteromedial edge (Fig. 23). Poorly separated medially except for posterior ¼ where slight increase in separa-

Fig. 22—*Uperoleia capitulata* sp. nov. (holotype). A, Lateral and B, Dorsal views of head. C, Palmar view of hand. D, Plantar view of foot. E, Dorsal view of frog showing hypertrophied glands.

tion present; not in bony or tenuous contact with sphenethmoid or with anterolateral extremities of frontoparietals. Maxillary process of nasal not developed—lateral extremity truncate, widely separated from shallow pars facialis of maxillary which lacks a preorbital process.

Palatines moderately robust, not extending laterally beyond lateral extremities of nasals; very slightly expanded medially, overlying anterior extremities of sphenethmoid along posterior half of proximal third of element (Fig. 23). Parasphenoid robust; cultriform process moderately broad, truncate, reaching anterior edge of sphenethmoid. Alary processes short, moderately broad, not overlain by medial rami of pterygoid. Medial rami of pterygoid short, robust, not in bony contact with prootic region; posterior rami short, broad; anterior rami in long contact with well-developed pterygoid process of palatal shelf of maxillary.

Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust and in firm contact with maxillary. Squamosal shaft robust, zygomatic ramus extremely short; otic ramus moderately long and slender, unexpanded. Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes, poorly separated medially, and with well-developed pterygoid processes.

Alary processes of premaxillaries slender, inclined medially and slightly anteriorly. Vomers absent. Bony columella present. Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles very slender, curved, closely applied medially. Coracoids moderately robust, widely separated medially, Scapula bicapitate, slightly shorter than clavicles. Suprascapula about ½ ossified.

Eight non-imbricate presacral vertebrae. Sacral

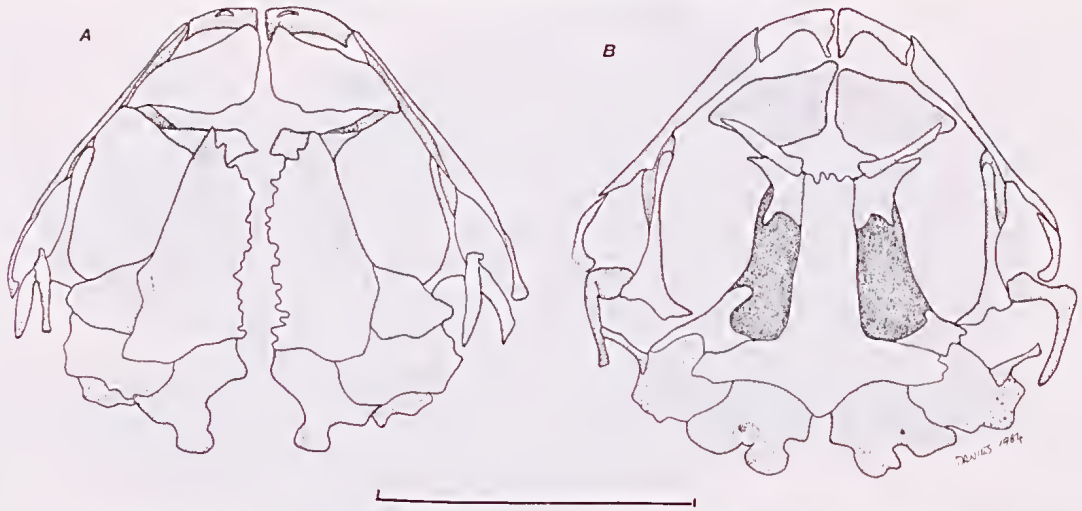

Fig. 23 — *Uperoleia capitulata* sp. nov. (SAM R29586). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

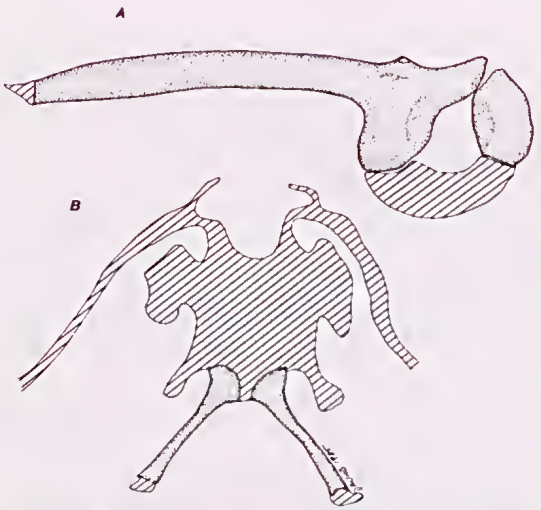

Fig. 24 — *Uperoleia capitulata* (QM J45960). A, Lateral view of the pelvic girdle. B, ventral view of the hyoid.

diapophyses poorly expanded. Relative widths of transverse processes III > II = saerum = IV > V > VI = VII = VIII. Bicondylar saeroeoeeygeal artieulation on urostyle. Well-developed erest extending ⅔ length of urostyle. No ilial erest; dorsal prominenee small, montieuline; dorsolateral dorsal protuberanee (Fig. 24). Pubis ealeified.

Humerus with strongly-developed anteroproximal erest. Phalangeal formula of hand 2,2,3,3. Carpus with five elements. Moderate torsion; O. radiale and O. ulnare present; O. radiale larger. Both elements artieulate with O. radioulna proximally, with eaeh other proximomedially and with large, transversely-elongate O. eentrale postaxiale distally. O. radiale artieulates laterally with O. eentrale preaxiale (Fig. 25). O. eentrale postaxiale artieulates distally with bases of O. metaearpi III, IV and V. Small flange extends proximally from lateroproximal eorner. Palmar sesamoid ventromedially (Fig. 25). O. eentrale preaxiale artieulates laterally with O. radiale, distally with O. eentrale postaxiale and with fused earpal elements of O. distale earpale 2 and 3, and laterally with basal prepollieal elements. Distal tips of terminal phalanges knobbed.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and O. fibulare elongate and fused at either end. O. tibiale extends to distal end of O. fibulare. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lies at base and slightly laterally to O. metatarsus II. Medial element lies at base of O. metatarsus I, artieulating also with O. eentrale prehallueis. Distal prehallieal element elliptie, extending approximately ⅓ length of O. metatarsus I (Fig. 25).

Hyoid plate slightly longer than broad. Anteromedial proeesses of anterior hyale short and slender (Fig. 24). Alary processes of hyoid plate not pedunculate. Posterolateral proeesses moderately broad, moderately long. Posterior eornua ossified.

VARIATION: A further five paratypes have been eleared and stained; QM J545960, J45958, SAM R29587, QM J26416, AM R28637.

The nasals are in tenuous eontact with the sphenethmoid in AM R28637 and QM J45958. The exposure of the frontoparietal fontanelle varies slightly in the paratypes. Exposure is never less than shown and is sometimes greater. In QM J26416 exposure is inereased by eontraetion of the frontoparietals about ⅔ along their length posteriorly.

The pars facialis of the maxillary is slightly deeper than in SAM R29586 in all the other skeletons. The palatines are not expanded medially other than in QM

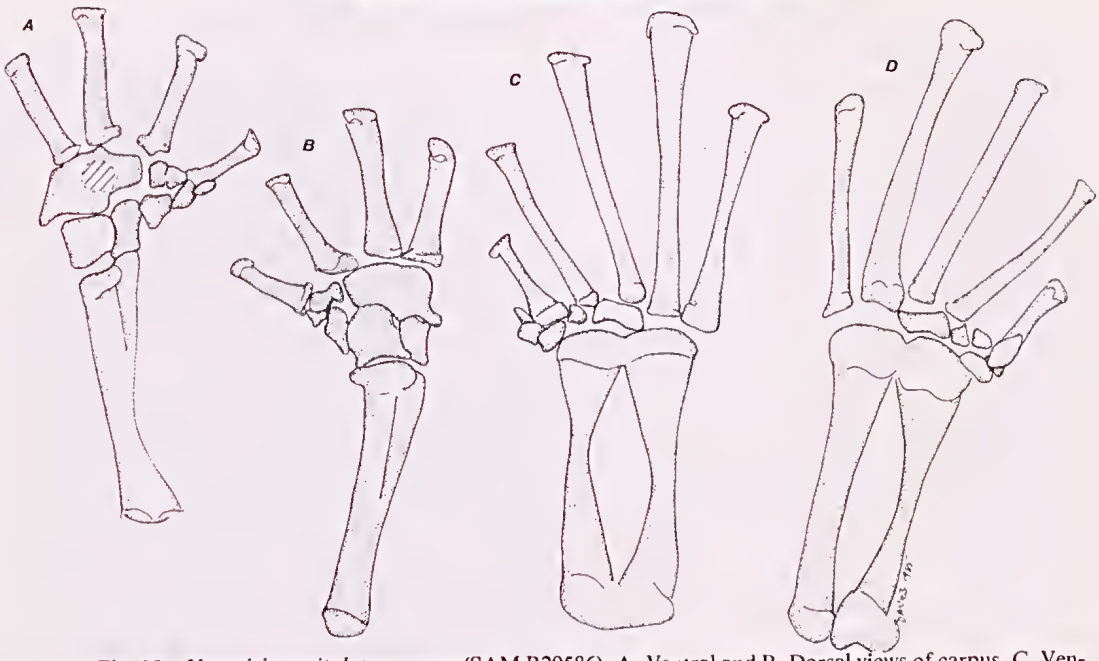

Fig. 25 — *Uperoleia capitulata* sp. nov. (SAM R29586). A, Ventral and B, Dorsal views of carpus. C, Ventral and D, Dorsal views of tarsus.

J26416. Vomerine fragments are present medial to the palatines in SAM R29587.

Habitat: Found in mulga woodland at Ambathala Nature Reference Site and in coolibah (*Eucalyptus microtheca*) lined waterholes at Noccundra.

Advertisement Call: The advertisement call of this species is not yet known.

Comparison with Other Species: *Uperoleia capitulata* is an untoothed species with a poorly-exposed frontoparietal fontanelle, features shared by some *U. lithomoda* and by *U. mimula.*

From *U. lithomoda* and *U. mimula, U. capitulata* is distinguished by its hypertrophied paratoid glands and relatively-smooth dorsum.

From the sympatric untoothed species *U. rugosa, U. capitulata* is distinguished by its hypertrophied dermal glands and greater exposure of the frontoparietal fontanelle.

Distribution: *Uperoleia capitulata* is confined to south western Qld and northwestern N.S.W., particularly in the Bulloo drainage system (Fig. 26). *U. capitulata* is sympatric with *U. rugosa* at some localities.

Etymology: From the Latin *capitulus* meaning having or ending in a small head, alluding to the characteristic feature of this species.

Comment: *Denisonia devisi* was observed feeding on this species at Range Tank, Ambathala Nature Reference Site.

Uperoleia fusca sp. nov.

Uperoleia marmorata: Moore 1961, p. 219 (part.); McDonald 1974, p. 2; Czechura 1978, p. 150; McEvoy, McDonald & Searle 1979, p. 176.

Uperoleia laevigata: Ingram & Corben 1975, p. 49.

Uperoleia sp.: Webber & Cogger 1976, p. 76; Thompson 1981, p. 94.

Holotype: SAM R29596, an adult male collected adjacent to southern boundary of Eungella N.P., 1.2 km along Crediton road from Broken River Crossing Qld (148°30′10″, 21°10′15″), by M. J. Tyler and K. R. McDonald on 26.i.1984.

Definition: A moderate-sized species (males 20-28 mm S-V, females 23-29 mm S-V) with a smooth dorsum; maxillary teeth present; toes unwebbed; frontoparietal fontanelle unexposed; ventral surface entirely pigmented; carpus of six elements; anteromedial processes of anterior hyale of hyoid in form of medial thickening; ilial crest absent; call a rasping note of about 20 pulses.

Description of Holotype: Maxillary teeth present. Vomerine teeth absent. Snout moderately short, rounded when viewed from above (Fig. 27), gently sloping posteriorly in profile (Fig. 27). Eye to naris distance very slightly greater than internarial span (E-N/IN 1.1). Nares dorso-laterally positioned. Canthus rostralis inconspicuous and straight. Loreal region straight. Tympanum not visible externally. Fingers moderately long, slender, unfringed, unwebbed with moderately-prominent subarticular tubercles but obscure palmar tubercles. In order of length 3>4>2>1 (Fig. 27). Hind limbs moderately long (TL/S-V 0.40). Toes long, very poorly fringed and unwebbed (Fig. 27). In order of length 4>3>5>2>1. Metatarsal tubercles small, inner rounded and flattened on axis of toe 1, outer small and conical, moderately acutely angled to the long axis of the foot. Subarticular tubercles small, not very prominent.

Dorsal surface faintly rugose (Fig. 28). Parotoid glands moderately developed, inguinal and coccygeal

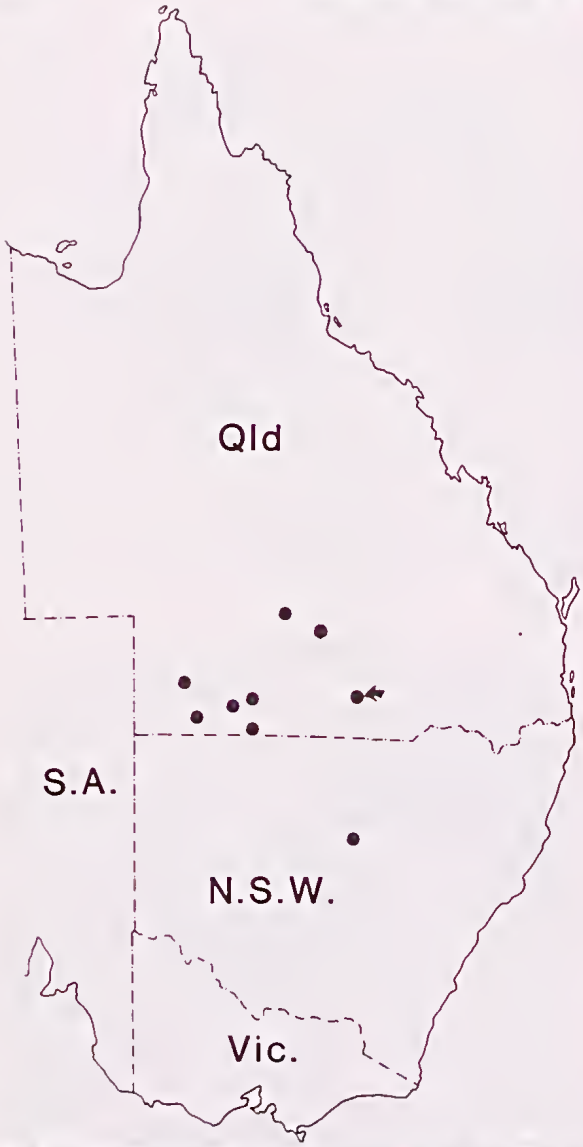

Fig. 26—Distribution of *Uperoleia capitulata* sp. nov. The arrow indicates the type locality.

glands not obvious. Submandibular gland disrupted. Cloacal flap with short fimbriations. Flap in anterior corner of eye. Ventral surface smooth.

Male with unilobular submandibular vocal sac. Dorsum grey in preservative with black and cream mottling. Entire ventral surface, including femoral regions pigmented with chocolate coloured patches of granules. Palmar surface of hand moderately pigmented, plantar surface of foot heavily pigmented. Throat darkly pigmented with paler diamond shaped patch at mandibular symphysis. Small, pale, post-femoral patch. Colour in groin and post-femoral patches reddish/orange in life. Nuptial pad unpigmented (Fig. 29).

DIMENSIONS (in mm): Snout-vent length 23; tibia length 9.3; eye diameter 2.9; eye-naris distance 2.0; internarial span 1.9.

VARIATION: There are 199 paratypes, 192 ♂♂ and 7 ♀♀.

N.S.W.: SAM R12590(12), Wyong, 1.6 km S, 9.6 km W of Ulong, F. Parker, H. Ehmann, P. Krauss, 26.i.1971; AM R15505-6, Boolamboyle, R. Mackay; AM R104374, R101331, 11 km from jcn with Pacific Hwy on Palm Grove Rd, Ourimbah, H. G. Cogger, 3.xi.1981; AM R4631-2. Worrell Ck, Nambucca River, W. Clark, 24.i.1910; AM R6301-2, Garavembi near Macksville on Nambucca River (30°44′, 152°59′), D. B. Fry and H. E. Smart, 1913; AM R53987-93, R53995-6, Erina, N. Dankers, 1974; AM R68438, 24.5 km N Colo Heights, Putty Rd (33°13′, 150°40′), P. Rankin and P. Greer, 15.xi.1975; AM R70200, 12.8 km along road to Wisemans Ferry from Kariong, R. Wellington, 25.i.1978; AM R115583 Whiteman Creek, S. J. Copland, 6.i.1948; NMV D25047-8, D25056-7, Ourimbah Creek, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 1.xi.1964; SAM R29597-8, same locality, M. Mahony, 3.xi.1981; AM R76508, same locality, D. O'Brien; NMV D25049-55, 10.4 km S Gloucester, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 29.x.1964; NMV D43207-10, 2.6 km N Coff's Harbour, G. F. Watson, D. F. Gartside, 11.xi.1972; NMV D25044-6 Nymboida, M. J. Littlejohn, 27.x.1964; NMV D43223, 17.6 km S Grafton, G. F. Watson, D. F. Gartside, 8.xi.1972; NMV D43247-8, D42679, D42681, 4.8 km SE Lower Creek on Kempsey-Armidale Rd, G. F. Watson, D. F. Gartside, 12.xi.1972; QM J40431, J40435, Undercliff, G. Czechura.

Qld: SAM R29599-602, QM J45961, collected with the holotype; SAM R29603-7, same locality, K. R. McDonald, 5.i.1976; KU 205027-8, same locality, K. R. McDonald, 4.ii.1975; AMNH 124732, same data, 28.i.1975; QM J31556-62, J31582 Eungella, C. Corben; AM R53809-11, 16 km S Eungella (21°17′, 148°36′), J. Barker, G. Grigg, 30.xii.1973; SAM R29608-11, QM J45962, CAS 160142-3, MCZ 108612-3, Bellthorpe S.F. (26°44′, 152°36′), K. R. McDonald, J. S. McEvoy, D. G. Crossman, 27.ii.1976; BMNH 1986.203, same locality, K. R. McDonald, P. Amos, 24.xi.1976; SAM R29612-3, same locality, K. R. McDonald, Jan. 1979; QM J45963-65, Jimna Rd nr Yielo turnoff, Sunday Creek S.F., K. R. McDonald, J. S. McEvoy, 5.i.1977; SAM R29614-6, Crows Nest N.P., K. R. McDonald, 14.i.1974; SAM R29617, Mt Glorious, C. J. Limpus, K. R. McDonald, 20.ii.1974; SAM R29618, 2 km from Sunday Creek turnoff along Jimna/Bellthorpe Rd (152°29′, 26°42′), K. R. McDonald, 13.xii.1978; SAM R29619, Moreton Is., nr Blue Lagoon swamp, K. R. McDonald, 16.ix.1976; QM J10901-2, Mt Nebo, S. Breedon, Feb. 1961; QM J10900, J12309, J12294, J12323, same data, 19.ii.1964; QM J42609, J42576, J42614, below Bombana N.P., Mt Nebo Rd (27°24′, 152°47′), C. Corben, A. Smyth, 31.x.1973; QM J19942, J19947, J19952, J19965, Dunwich, North Stradbroke Is., 1. R. Straughan; QM J24088, Brown Lake, North Stradbroke Is., G. Ingram, G. Czechura, 5.iv.1974; QM J27563, Blue Lake, North Stradbroke Is., D. Grace, 2.i.1976; QM J27905, same locality, A. Elliot, M.

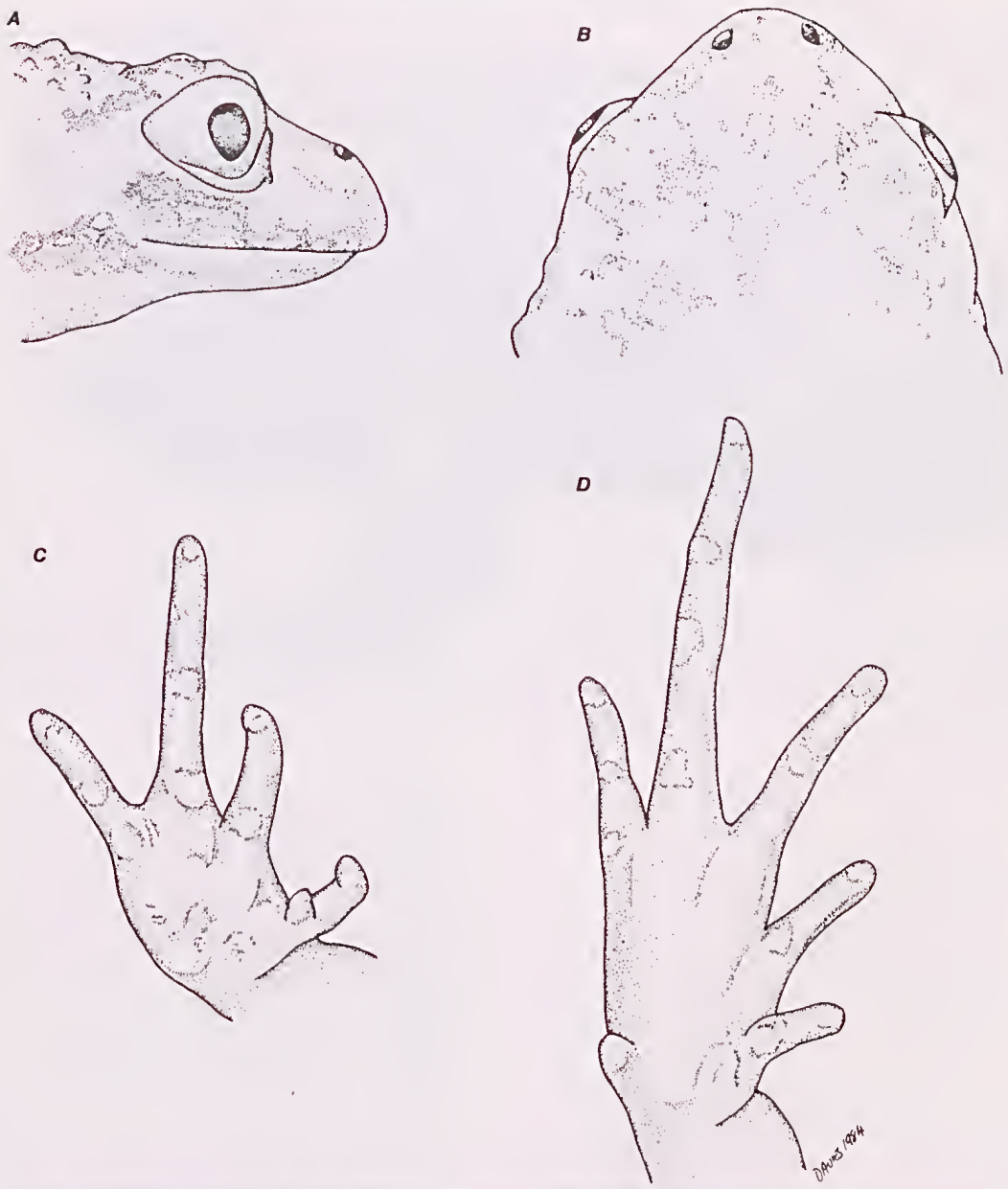

Fig. 27 — *Uperoleia fusca* sp. nov. (holotype). A, Lateral and B, Dorsal view of head. C, Palmar view of hand. D, Plantar view of foot.

Hillier, 10.v.1976; QM J40020, Tortoise Lagoon, Blue Lake area (21°08′, 148°29′), L. Kading, 22.x.1981; QM J42569, J42572, J42583, J42606-7, Brown Lake, North Stradbroke Is., C. Corben *et al.*, 8.ix.1973; QM J42593, same data, 15.ix.1973; QM J19925, J19927, J19930, J19936, J19959, J19961, J19966, Slacks Creek, Pacific Hwy, I. R. Straughan, 9.x.1961; QM J40433, Cooloola, G. Czechura, 1.i.1974; QM J27477, J27475, Lake Cooloomera, Cooloola, C. Corben, A. Smyth, 21.xi.1973; QM J42586-90, QM J42610, J42612, same locality, G. Ingram, 14.vii.1973; QM J27481, same locality, G. Ingram, G. Czechura, 30.xii.1973; QM J42564, J42566-68, J42574-5, J42578-9, J42581, J42585, J42591-2, J42594, J42596, J42599-603, J42611, same locality, C. Corben *et al.*, 15.ix.1973; QM J39315, Poona Lake, Cooloola N.P., G. Monteith, Jan. 1981; QM J42565, J42570-1, J42573, J42580, J42584, J42595, J42604-5, J42608, J42613, Lost World (28°15′, 153°07′), C Corben *et al.*, 28.vii.1973; QM J42563, J42597-8, J42582, Calam Rd, Runcorn (27°36′, 153°04′) C. Corben, G. Ingram, 10.x.1973; QM J40434, Maleny, G. Czechura, Feb. 1974; QM J40489-90, same data, 13.iv.1974; QM J40486-7, same data, April 1974; QM J40484, same data, 26.ix.1974; QM J41533, Pine Creek

Fig. 28—*Uperoleia fusca* sp. nov. in life (Topotype).

Timber Reserve south of 'Turkey' nr Miriamvale, T. Pulsford, 10.i.1983; QM J19938, J19953, J19957, Mt Tamborine, I. R. Straughan, 27.ix.1964; QM J18817, J18825, Moggill Rd, 8 km past Kenmore P.O., Brisbane, I. R. Straughan and A. K. Lee, 26.i.1961; QM J18837, Gold Creek Rd, 1.6 km past Brookfield turnoff, Brisbane, A. K. Lee, 26.ii.1961; QM J18822, Sampsonvale, A. K. Lee, 13.viii.1961; QM J29280, Kileoy, G. Czechura, Nov. 1976; QM J19956, Warrawee, I. R. Straughan, 1.iii.1964; QM J19939, J19941, Brookfield Showground, Moggill Rd, Brisbane, A. K. Lee, 9.x.1961; QM J19943, 16 km N Gayndah, I. R. Straughan, 17.x.1963; QM J40315, Deepwater Rd, south of township '1770', T. Pulsford, 1.iv.1972; QM J30606, Ravensbourne, R. Sadlier, 7-8.i.1978; QM J18832, 3.2 km N Tamborine Village on Tamborine-Waterford Rd, I. R. Straughan, 12.ix.1964; QM J12721, Eidsvold, T. L. Bancroft, 30.viii.1912; QM J19958, 16 km N Cooroy, I. R. Straughan, 17.x.1963; AM R47734, R47736-7, Eurimbula E of Miriamvale, P. Webber.

Many of the male paratypes exhibit well-defined glandular, unpigmented nuptial pads (Fig. 29). Pigmentation of the ventral surface of the hands makes the pads particularly prominent in this species. Paratypes are all long-legged frogs [TL/S-V 0.38 ± .02, (0.35-0.42)]. Eye to naris distance approximates internarial span in most paratypes [E-N/IN 1.18 ± .17, (0.88-1.67)]. The gentle

Fig. 29—Palmar view of hand of *Uperoleia fusca* sp. nov. showing unpigmented subepidermal nuptial pad (SAM R29618).

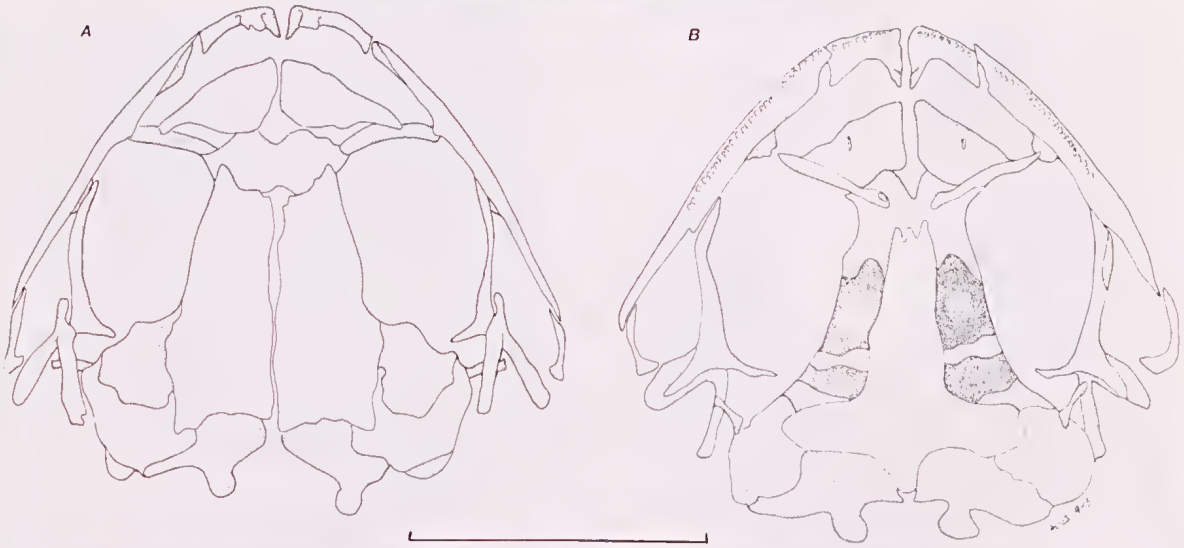

Fig. 30—*Uperoleia fusca* sp. nov. (SAM R29603). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

posterior slope of the snout of the holotype in lateral view, is characteristic of all paratypes.

All but three of the paratypes lack a distinct palmar tubercle at the base of the thumb. In the exceptions, the tubercle is better defined, but not prominent. Only four paratypes have toe fringing greater than in the holotype.

Dorsal patterning varies; some specimens are uniformly dark slate and others have bold chocolate patterning on a grey or brown background; many specimens exhibit an indistinct triangular preocular patch characteristic of the other toothed eastern Australian congeners. A pale midvertebral stripe occurs occasionally and many paratypes exhibit heavier ventral pigmentation than the holotype. Ventral pigmentation ranges from faint suffusions on a cream background to light speckles on a chocolate or slate background. Fading of pigmentation in preservative is common in this genus. Of the specimens with lighter ventral pigmentation, the pigment is spread uniformly across the entire ventral surface.

In life there is a dichotomy in inguinal and postfemoral colour. Where recorded (AM R6302, NMV D43247-8, SAM R29608-11) thigh colour at the southern part of the range of the species is yellow but in the northern part of the range is reddish/orange. Both thigh colours were recorded in specimens calling at a pool in the Conondale Ranges (SAM R29608-9, yellow thighed and SAM R29610-11 reddish/orange). The calls of these two forms were indistinguishable to the ear (K. R. McDonald unpubl.) and there are no morphological distinctions between the four specimens.

Osteology (based on SAM R29603): Skull well ossified, sloping slightly anteroventrally. Ossification of sphenethmoid complete medially, dorsally extends to posterior extremities of nasals, ventrally extends about ⅓ length of orbit posteriorly. Prootic not fused with exoccipital (Fig. 30). Epiotic eminences prominent. Exoccipital not ossified dorsomedially or ventromedially. Crista parotica short, stocky, not articulating with long otic ramus of squamosal. Shallow groove for carotid canal present posteriorly on frontoparietals. Frontoparietal fontanelle exposed only as a median slit between the well-ossified frontoparietal elements. Anterior extremity about level of anterior ramus of pterygoid. Posterior extremity undefined.

Nasals moderately ossified, triangular, closely applied medially with slight separation posteriorly (Fig. 30); in tenuous contact with sphenethmoid. Maxillary process of nasal poorly developed, not in bony contact with well-developed preorbital process of shallow pars facialis of maxillary. Palatines moderately broad, slightly reduced and truncated laterally from level of dorsal extremity of preorbital process of pars facialis of maxillary (Fig. 30); angled at about 45° to overlay sphenethmoid medially.

Parasphenoid robust. Cultriform process moderately broad, not reaching level of palatines. Alae robust, deep, not angled to cultriform process; not overlapped nor reaching extremity of medial ramus of pterygoid. Medial ramus of pterygoid slender, acuminate, not in bony contact with prootic region. Posterior ramus moderately long, slender; anterior ramus in moderately-long contact with moderately-developed pterygoid process of palatal shelf. Small cartilaginous quadrate present at base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal shaft robust, short, knobbed, zygomatic ramus, long unexpanded otic ramus.

Maxillary and premaxillary dentate. Palatal shelf moderately deep with well-developed palatine processes, not abutting medially, and poorly- to moderately-developed pterygoid process. Alary processes of premaxillaries moderately slender, poorly bifurcated dorsally, slightly curved posteriorly. Pars facialis of

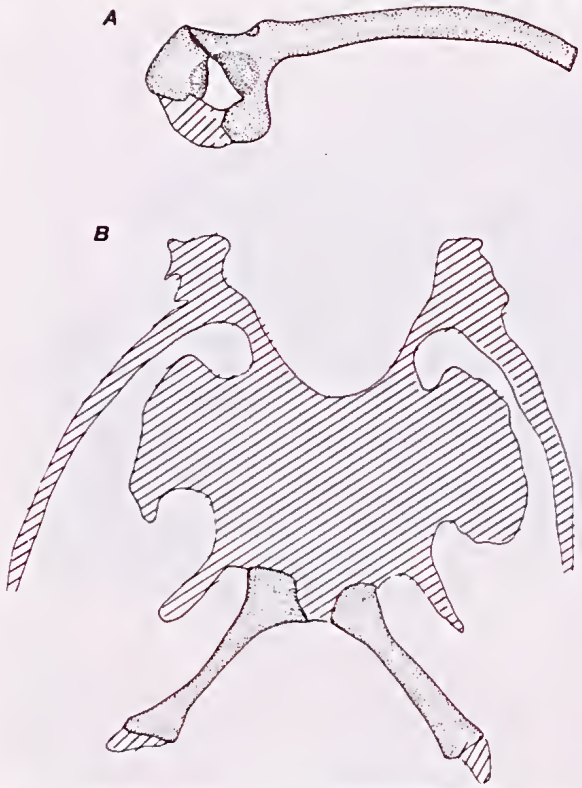

Fig. 31—*Uperoleia fusca* sp. nov. (SAM R29607). A, Lateral view of ilium. B, ventral view of the hyoid.

maxillary deep then stepped down to become shallow. Preorbital process prominent. Remnant fragments of vomers on edges of choanae and extremities of palatines (Fig. 30). Bony columella present.

Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids robust, widely separated medially. Scapula bicapitate, about same length as clavicles. Suprascapula about ½ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Left ilium abnormally enlarged at distal end. Relative widths of transverse processes III > II = saerum = IV > V = VI = VII = VIII. Crest on urostyle for about ⅓ its length. Ilium with no dorsal crest. Dorsal prominence very small, slightly rounded with rounded posterolateral dorsal protuberance (Fig. 31). Pubis calcified.

Humerus with strongly-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Distal tips of terminal phalanges knobbed. Carpus of six elements; moderate torsion. O. ulnare and O. radiale present. O. radiale larger of two; both articulate with O. radioulna proximally and with each other medially. Distally both articulate with large transversely-elongate O. centrale postaxiale. O. radiale articulates laterally with O. centrale preaxiale (Fig. 32). O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Moderately well-developed flange extends slightly laterally from lateroproximal corner. Palmar sesamoid anteroventrally. O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with unfused carpal elements of O. distale carpale 2 and 3 and laterally with basal prepollical element.

Phalangeal formula of foot, 2,2,3,4,3. O. tibiale and O. fibulare elongated elements fused at either end. O. tibiale extends as far as distal end of O. fibulare. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III, extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lies at base of O. metatarsus II. Medial element lies at base of O. metatarsus I, articulating also with O. centrale prehallucis. Distal prepollical element slender and short extending for about ⅓ length of O. metatarsus I (Fig. 32).

Hyoid plate slightly longer than wide. Anterior hyale expanded anteromedially (Fig. 31). Alary processes not pedunculate. Posterolateral processes moderately slender and elongate. Posterior cornua ossified. Some medial calcification of plate between posterior cornua.

Variation: Seventeen of the paratypes have been examined for osteological variation: SAM R29606-7, R29599, R29612-3, R29619, KU 205027, QM J18832, J19927, J27475, J42579, J42598, J42606, J42608, NMV D25045, D25048, D43208.

Medial ossification of the sphenethmoid is incomplete in all of these paratypes. Tenuous contact between the nasals and the sphenethmoid is exhibited by only two paratypes. Separation of the nasals posteromedially varies: in about ⅓ of the specimens the separation is more extreme and in three specimens it is less than described. The epiotic eminences are extremely prominent in all paratypes except the subadult SAM R29619.

The nature of the pars facialis of the maxillary varies—in some paratypes the shelf is deep initially and then steps down to be shallow anteriorly, in others the decline in depth is gradual and in one specimen (NMV D25048) it remains deep for its entire length.

The alary processes of the premaxillaries are usually moderately broad, but occasionally are broad. Bifurcation of the dorsal extremity varies considerably. The palatines are uniformly truncated laterally. The presence of vomerine fragments varies—they occur in about ⅓ of the paratypes but the palatal elements are not always apparent bilaterally and in QM J42606 they are relatively large.

In two specimens, the alae of the parasphenoid are curved posterolaterally.

The anterior extremities of the frontoparietals are reduced medially and the frontoparietal fontanelle is barely exposed or unexposed except in the subadult SAM R29619.

Advertisement Calls: Calls of five individuals were recorded at the type locality on 26.i.1984. Call parameters are shown in Table 3 and an advertisement call is shown in Fig. 33. The call is a short rasping note with a duration of about 300 ms pulsed at about 68

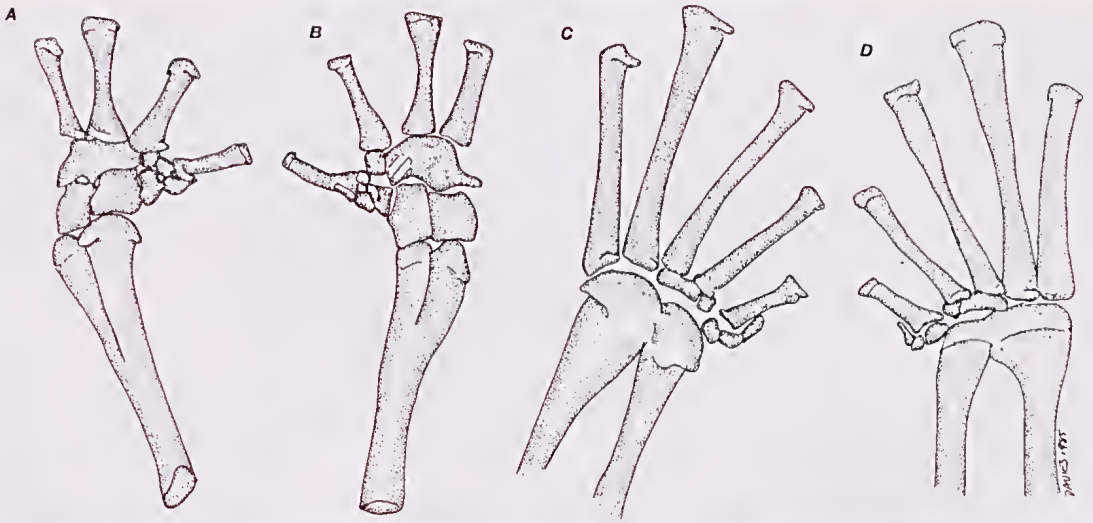

Fig. 32—*Uperoleia fusca* sp. nov. (SAM R29603). A, Dorsal and B, Ventral views of carpus. C, Dorsal and D, Ventral views of tarsus.

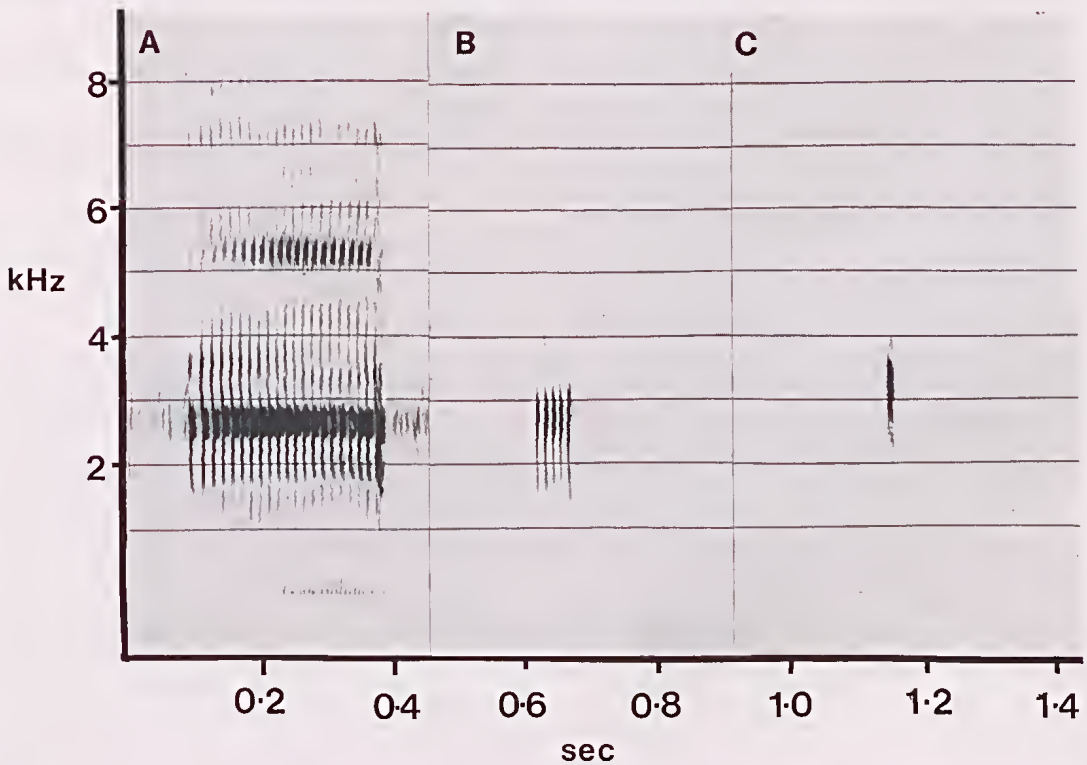

Fig. 33—Sonagrams of advertisement calls. A, *Uperoleia fusca* sp. nov. (QM J45961). B, *Uperoleia mimula* sp. nov. (QM J45943). C, *U. lithomoda* (SAM R28771).

Fig. 34—Type locality of *Uperoleia fusca* sp. nov.

pulses sec^{-1}. The dominant frequency lies at about 2700 Hz.

HABITAT: The type locality was a small pond, 30×30 m, surrounded by dry ground covered with sparse low grass to a height of little more than 15 cm (Fig. 34). Frogs were calling at the base of the grass (M. J. Tyler Field notes). The type locality, Mt Glorious, and the Conondale Ranges sites are tall open eucalypt forest with *Themeda australis* understorey. Other localities are open forest with tussock grass understorey except Poona Lake which is surrounded by tall shrubland.

COMPARISON WITH OTHER SPECIES: *Uperoleia fusca* is a moderate sized species (males 20-28 mm S-V, females 23-29 mm S-V), with maxillary teeth and with a poorly-exposed frontoparietal fontanelle. These features are shared by *U. marmorata* and *U. laevigata*. From *U. marmorata*, *U. fusca* is separated by size (*U. marmorata*, ♂ 30.1 mm) and by its narrower snout (E-N/1N 1.18±.17 in *U. fusca*, 1.56 in *U. marmorata*).

From *U. laevigata*, *U. fusca* is separated by total pigmentation of the ventral surface (absent in *U. laevigata*) and by call. The call of *U. fusca* has 11-28 pulses whereas that of *U. laevigata* is a longer call of 32-56 pulses (Davies & Littlejohn 1986).

DISTRIBUTION: *Uperoleia fusca* is a coastal species ranging from Gloucester in N.S.W. (32°01′, 151°58′) to Eungella in Qld (20°55′, 148°30′) (Fig. 35). Toothed specimens from Atherton held by the Queensland Museum may be referrable to this species, but unfortunately are in such poor condition that identification is impossible.

ETYMOLOGY: From the Latin *fuscus* meaning dusky with reference to the ventral pigmentation of the species.

Uperoleia littlejohni sp. nov.

HOLOTYPE: QM J45949 (formerly QNPWS N56317), an adult male collected on Occupational licence 410, Burra Range, Qld (20°33′, 145°05′) by B. C. Lawrie on 14.xii.1983.

DEFINITION: A moderately-large species (males 22-31 mm S-V, females 23-29 mm S-V) lacking maxillary teeth; possessing unwebbed and poorly-fringed fingers and basal to no webbing and fringed toes. Dermal glands are prominent. Frontoparietal fontanelle moderately extensive; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Call not known.

DESCRIPTION OF HOLOTYPE: Maxillary teeth absent. Vomerine teeth absent. Snout short, truncated when viewed from above and in profile. Eye to naris distance greater than internarial span (E-N/1N 1.25) (Fig. 36). Canthus rostralis poorly defined, straight. Tympanum not visible externally (Fig. 36).

Fingers moderately long, broad, unwebbed and poorly fringed with very prominent subarticular tubercles (Fig. 36). In order of length 3>4>2>1. Palmar tubereles large and prominent. Hind limbs moderately long (TL/S-V 0.34). Toes moderately long,

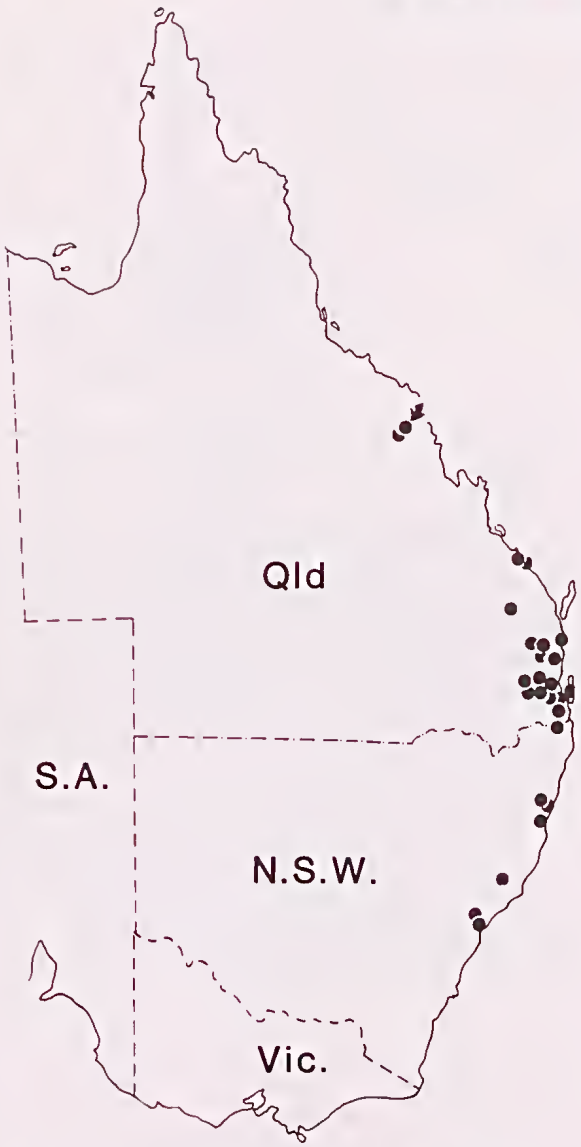

Fig. 35—Distribution of *Uperoleia fusca* sp. nov. The arrow indicates the type locality.

broadly fringed with basal webbing. Toes in order of length 4>3>5>2>1. Metatarsal tubercles very large, raised and prominent; outer elongate, truncate and angled to long axis of foot; inner acutely angled along toe 1 (Fig. 36).

Dorsal surface very faintly tubercular. Parotoid, inguinal and coccygeal glands moderately developed. Submandibular gland disrupted. Cloacal flap slightly fimbriated. Ventral surface faintly granular.

Male with unilobular submandibular vocal sac; unpigmented glandular nuptial pad on thumb. Dorsum grey in preservative with strong chocolate markings, and pinkish-tipped tubercles. Parotoid glands pinkish and inguinal and coccygeal glands with disrupted pinkish patches. Inguinal and post femoral patches white. Ventral surface whitish with suffusions of brown pigment. Throat grey with white granules.

Dimensions (in mm): Snout-vent length 27.6; tibia length 9.5; eye diameter 3.0; eye-naris distance 2.0; internarial span 1.6.

Variation: There are 26 paratypes, 24 ♂♂ and 2 ♀♀. All are from Qld. QM J38877-80, 22.4 km W Pentland (20°40′, 145°18′), G. Ingram, G. Czechura 15.i.1981; QM J45950, Epping Forest N.P. near Clermont (22°23′, 146°42′), G. Porter, D. G. Crossman 12.ix.1984; SAM R29620-1, Gorge Ck (19°33′, 143°56′), A. Taplin 18.iii.1984; QM J38883, 18.1 km W Torrens Ck, G. Ingram, G. Czechura 15.i.1981; QM J45953, Battery Station, Snake Creek (145°39′, 19°27′), B. C. Lawrie 2.xii.1981; SAM R29622, QM J45952, Caerphilly Station (21°03′, 146°05′), B. C. Lawrie 3.iii.1981; KU 205029, CAS 160144, MCZ 108614, QM J45954, SAM R29623, Strathtay (20°57′, 144°12′), B. C. Lawrie 24.viii.1984; QM J45951, SAM R29624, Amber Station, about 1.6 km from Frenchs Crossing on Lynd River, K. R. McDonald, S. K. Reardon 15.i.1980; SAM R29625-6, Walsh River, Watsonville (17°21′, 145°18′), J. W. Winter 24.xii.1973; QM J43154-5, Walsh River, Jamie Creek, Watsonville, 15.xii.1973; QM J38915, Crest of Warrigal Ra, 16.8 km E Cloncurry, G. Ingram, G. Czechura, 18.i.1981; QM J29874, 96 km from Townsville on Charters Towers Rd, G. Ingram, D. Miller 22.xii.1976; AM R53930, R53932, 6.4 km W Herberton (17°23′, 145°23′), J. Barker, G. Grigg 10.i.1974.

All paratypes are moderately robust, slate grey frogs with strong back patterning and conspicuous dermal glands. Paratypes have moderately-long limbs [TL/S-V 0.35 ± .02 (0.32-0.41)]. Males range 21.6-30.7 mm S-V and females 23.2-28.8 mm S-V. Eye to naris distance is always greater than internarial span [E-N/IN 1.35 ± .25, (1.01-1.64)]. The dorsum is more rugose in a few paratypes and the dermal glands, particularly the coccygeal glands, are more prominent. The parotoid glands are extremely well developed in the larger female (QM J45950). Most of the paratypes, particularly those that are relatively freshly-preserved, show the characteristic salmon pink colouration on the dermal glands and on the tips of dorsal tubercles. The ventral surface is usually a very pale grey with varying suffusions of brown pigment. Colour is apparent in the inguinal and post femoral patches. A pale midvertebral stripe is apparent in some specimens.

Osteology (based on SAM R29623): Skull poorly ossified, sloping slightly anteroventrally. Sphenethmoid not ossified medially. Small portion of sphenethmoid ossified posteriorly to anterior extremity of cultriform process of parasphenoid extending about ⅓ to ½ of length of orbit in ventral view. Prootic not fused with exoccipital. Exoccipital not ossified dorso- or ventromedially. Crista parotica short and stocky, not overlain laterally by otic ramus of squamosal. Very shallow groove of carotid canal posterolaterally on frontoparietals. Frontoparietal fontanelle moderately extensively exposed, vase shaped (Fig. 37). Anterior margin

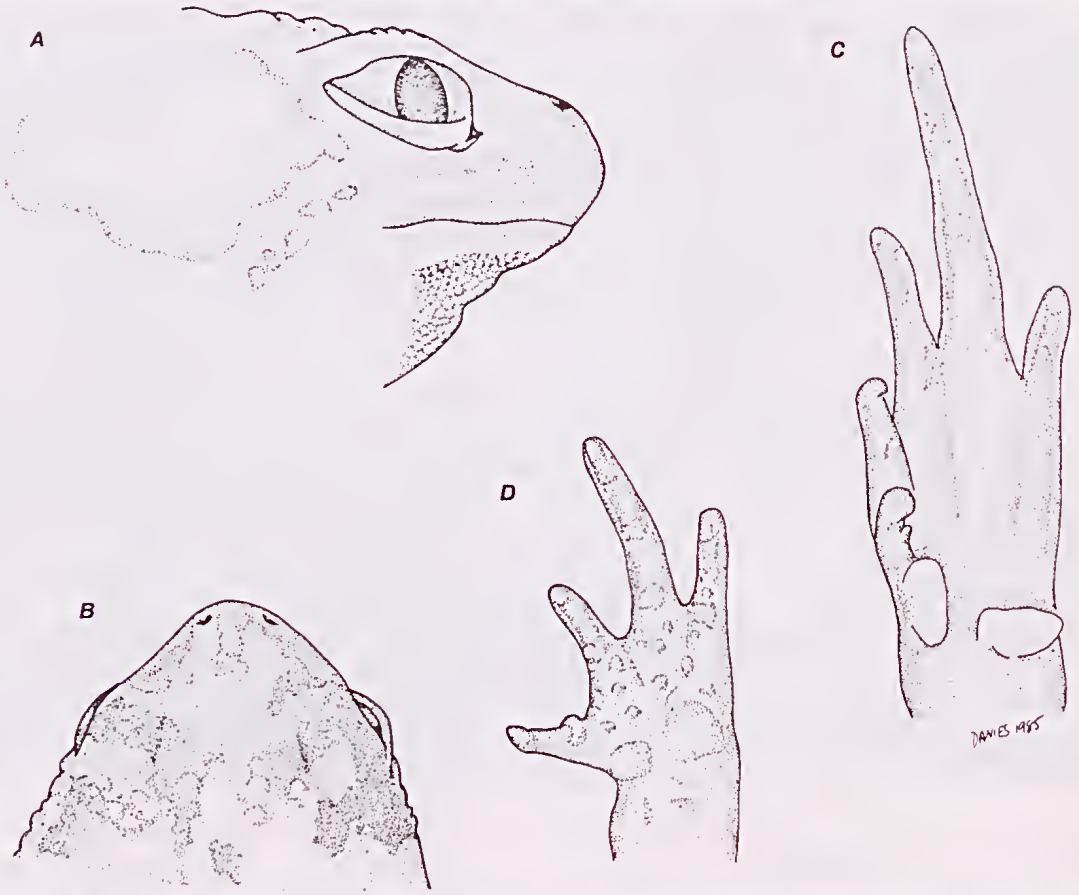

Fig. 36—*Uperoleia littlejohni* sp. nov. A, Lateral and B, Dorsal views of head (QM J38877). C, Plantar view of foot. D, Palmar view of hand (QM J45950).

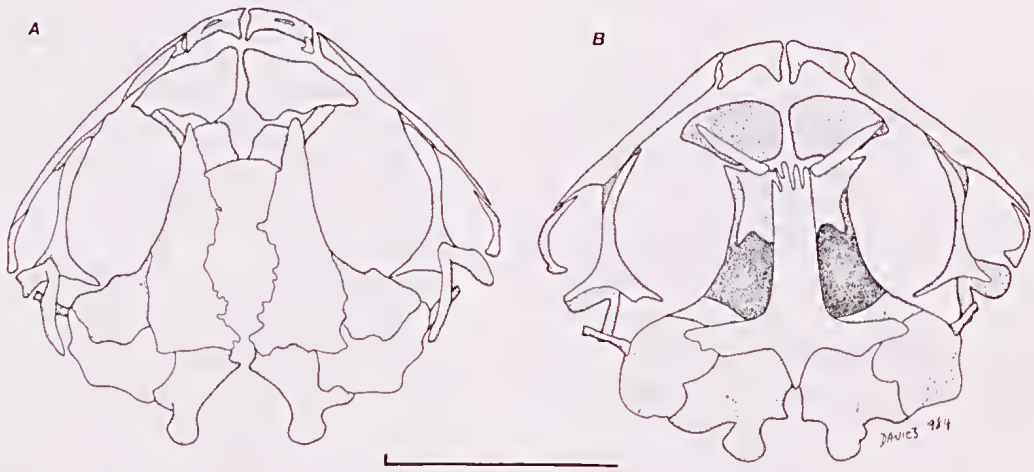

Fig. 37—*Uperoleia littlejohni* sp. nov. (SAM R29623). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

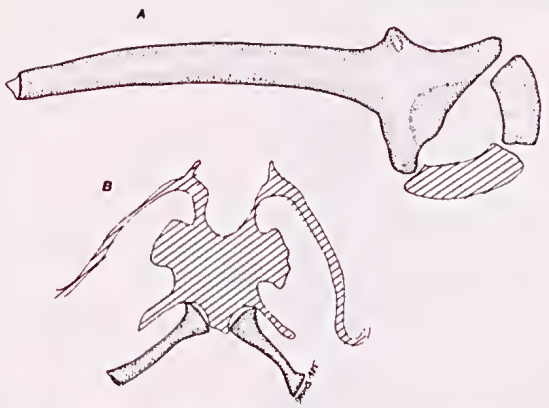

Fig. 38—*Uperoleia littlejohni* sp. nov. (QM J45954). A, Lateral view of ilium. B, Ventral view of hyoid.

defined by sphenethmoid at level about ¼ posterior on length of orbit. Posterior margin undefined because of lack of medial ossification of exoccipitals.

Nasals moderately large, approximately triangular. Directed ventrally on lateral extremities; slightly crescentic on medial anterior edge; in tenuous contact with sphenethmoid posteromedially. Not in contact with frontoparietals. Maxillary processes of nasals truncate, not in contact with moderately-shallow pars facialis of maxillary.

Palatines moderately slender, slightly expanded medially, angled acutely to sphenethmoid (Fig. 37) and totally underlying nasals. Parasphenoid robust. Cultriform process moderately broad, long, anterior extremity divided into digitiform processes (Fig. 37) extending to level of medial extremities of palatines. Alae moderately narrow, at right angles to cultriform process, not overlapped by medial rami of pterygoids.

Medial rami of pterygoids short, acuminate, not in bony contact with prootic region. Posterior ramus short, moderately broad. Anterior ramus in long contact with well-developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate between base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Shaft of squamosal stocky. Zygomatic ramus not developed; otic ramus long, unexpanded.

Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes not abutting medially. Pterygoid process well developed. Alary processes of premaxillaries broad at base, narrowing dorsally, bifurcate dorsally, inclined slightly medially. Pars facialis of maxillary moderately shallow; no preorbital process developed. Vomers absent. Bony columella present.

Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids robust, poorly separated medially. Scapula about equal in length to clavicles. Suprascapula about ½ ossified.

Eight nonimbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes III > II > sacrum > IV = V = VI = VII > VIII. Transverse processes on vertebra IV are curved posteriorly. Bicondylar sacrococcygeal articulation. Well-developed crest extending about ½ length of urostyle. Ilial crest absent. Dorsal prominence mon-

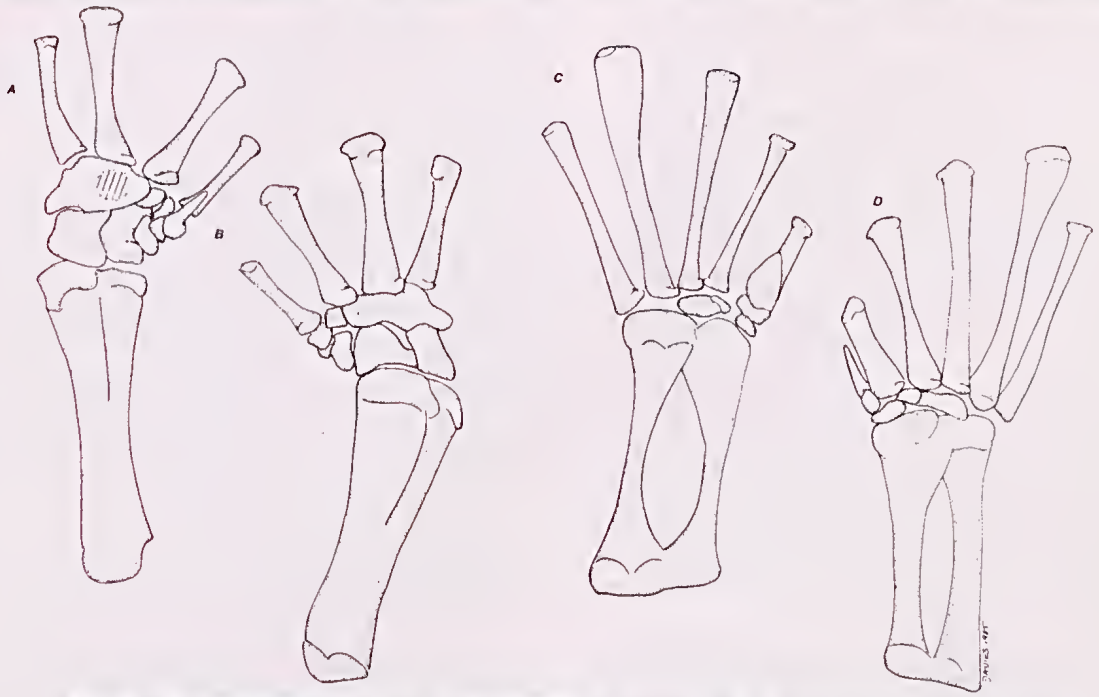

Fig. 39—*Uperoleia littlejohni* sp. nov. (SAM R29622). A, Ventral and B, Dorsal views of carpus. C, Ventral and D, Dorsal views of tarsus.

ticuline; dorsal protuberance mediolateral and prominent (Fig. 38). Pubis clacified.

Humerus with well-devcloped anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus of six elements. Moderate torsion. O. radiale and O. ulnare present. O. radiale larger of two. Both articulate with O. radioulna proximally and with cach other proximomedially. Distally both articulate with large transverscly-clongate O. centrale postaxiale. O. radiale articulates latcrally with O. centrale preaxiale. O. centrale postaxiale articulates distally with bascs of O. metacarpi III, IV and V. Small rounded flange extends proximally onto latcral surface of O. ulnare from lateroproximal corner. Palmar sesamoid ventromedially (Fig. 39). O. centrale preaxiale articulates latcrally with O. radiale, distally with O. centrale postaxiale and with carpal elements of O. distale carpale 2 and 3, and laterally with basal prepollical element (Fig. 39). Terminal phalanges knobbed.

Phalangeal formula of foot, 2,2,3,4,3. O. tibialc and O. fibularc elongate, fused at each end. O. tibialc extends to distal end of O. fibularc. Three distal tarsal elements. Lateral element largest, at base of O. metatarsus III; extcnds laterally to articulate with mediproximal side of basc of O. metatarsus IV and medially to base of O. metatarsus II. Second clemcnt at base of O. metatursus II. Mcdial element at base of O. metatarsus I, articulating with O. centrale prehallucis (Fig. 38). Distal prehallical elcment broad and elongate extending greater than ½ length of O. metatarsus I (Fig. 39).

Hyoid plate about as broad as long. Alary processcs not pedunculate, moderately broad. Posterolateral processes moderately long and slender. Anteromedial processes of anterior hyale slender. Posterior cornua ossified (Fig. 37).

VARIATION: Nine additional paratypes havc bccn cleared and stained. SAM R29622-4, QM J35427, J45953, J29874, J38880, J38883, AM R53930.

None of the cleared and stained specimens have a preorbital process on thc pars facialis of thc maxillary. The pars facialis is usually slightly deeper than in the described specimen and occasionally sculpturcd (QM J29874, SAM R29622). The nasals are not in tenuous contact with the sphenethmoid in QM J38880 and AM R53930, but overlay the sphenethmoid in the two very large specimens SAM R29622, QM J35427. The frontoparietal fontanelle exposure is as described in all but the two large specimens in which the medial constriction is accentuated and the degrec of exposure is lcss overall.

Vcntrally the acute anglc of the palatines is constant, but the digitiform naturc of the extremity of the cultriform process of thc parasphenoid is not always present. In one specimen (SAM R29624), the alae of thc parasphenoid are angled slightly posterolaterally.

ADVERTISEMENT CALL: The call of this species is not yet known.

COMPARISON WITH OTHER SPECIES: *Uperoleia littlejohni* is an untoothed specics with a moderately widely-exposed frontoparictal fontanelle, featurcs shared by *U. crassa, U. talpa, U. russelli, U. glandulosa, U. borealis, U. arenicola, U. inundata* and *U. orientalis.*

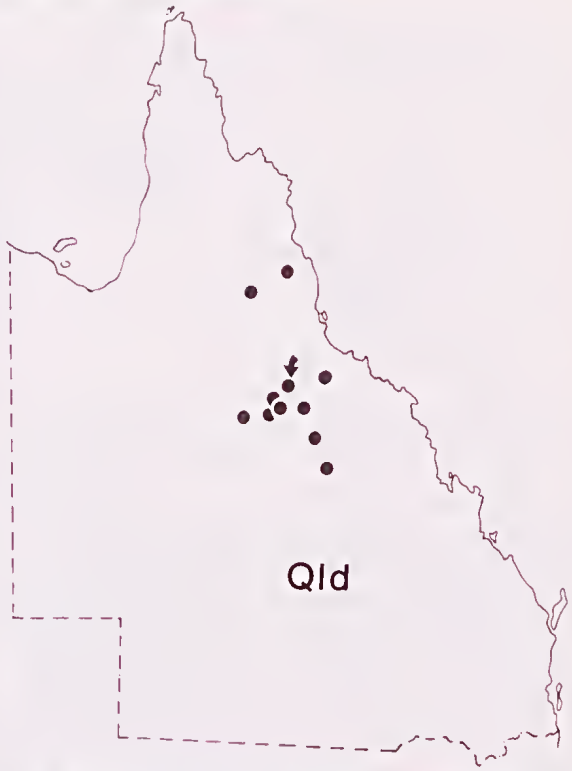

Fig. 40—Distribution of *Uperoleia littlejohni* sp. nov. The arrow indicates the type locality.

From U. talpa, U. russelli, U. borealis and *U. orientalis, U. littlejohni* is distinguished by the lack of modcrate webbing betwcen the tocs. From *U. glandulosa, U. littlejohni* is distinguishcd by the absence of ventral pigmentation, othcr than faint suffusions and by the absence of lyrate markings on thc dorsum and of a well-developed preorbital process of the pars facialis of the maxillary.

From *U. inundata, U. arenicola* and *U. crassa, U. littlejohni* is distinguished by its strong markings on the dorsum, and by thc absence of a preorbital process on thc pars facialis of the maxillary.

DISTRIBUTION: *Uperoleia littlejohni* is known only from north eastern and north central Queensland betwecn latitudes 17°-21° (Fig. 40).

ETYMOLOGY: The species is named for Murray J. Littlejohn of the University of Mclbourne in rccognition of his contributions to thc study of hcrpetology in Australia and of *Uperoleia* in particular.

Uperoleia mimula sp. nov.

Uperoleia marmorata: Parker & Tanner 1971, p. 5.
Uperoleia sp.: Mcnzies 1977, p. 21; Zweifel & Tyler 1982, p. 764.
U. lithomoda: Tyler & Davics 1984, p. 123 (part.).

HOLOTYPE: QM J45943 (formerly QNPWS N28874), an adult male collected at Lakcfield Ranger Station (14°56′, 144°12′) by K. R. McDonald and B. J. Lyon on 25.ii.1981.

Fig. 41 – *Uperoleia mimula* sp. nov. (holotype). A, Lateral and B, Dorsal views of head. C, Plantar view of foot. D, Palmar view of hand.

DEFINITION: A small to moderate-sized species (males 20-28 mm S-V, females 21-28 mm S-V) with a faintly rugose dorsum; moderately well-developed inguinal glands; toe webbing absent or basal; maxillary teeth absent; poorly- to moderately-exposed frontoparietal fontanelle; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent; male advertisement call a pulsed click of 4-5 pulses, with a pulse repetition rate of about 79 pulses sec^{-1}.

DESCRIPTION OF HOLOTYPE: Maxillary teeth absent. Vomerine teeth absent. Snout short, slightly pointed when viewed from above (Fig. 41), rounded in profile (Fig. 41). Eye to naris distance greater than internarial span (E-N/IN 1.36). Canthus rostralis inconspicuous and straight. Nostrils dorsolateral, surrounded by elevated lip (Fig. 41). Tympanum not visible externally (Fig. 42).

Fingers moderately long, slender, unwebbed, very slightly fringed with prominent subarticular tubercles. In order of length 3>4=2>1 (Fig. 41). Palmar tubercles moderately large but not prominent. Hind limbs short (TL/S-V 0.34). Toes long, moderately fringed with trace of basal webbing. Toes in order of length 4>3>5>2>1 (Fig. 41). Metatarsal tubercles prominent. Inner rounded, lying along axis of toe 1; outer rounded, acutely angled to long axis of foot.

Subarticular tubercles moderate, slightly conical. Dorsal surface tubercular. Parotoid glands moderately developed; inguinal glands well developed; coccygeal glands prominent. Submandibular gland small, not discrete. Cloacal flap tiny, not fimbriated. Ventral surface faintly granular. Male with unilobular, submandibular vocal sac. Cream glandular nuptial pad on thumb.

Dorsum grey in preservative with faint chocolate patterning and cream tipped tubercles. Prominent midvertebral stripe. Inguinal glands with cream patches along length. Inguinal and femoral patches scarcely detectable, cream. Ventral surface cream with very faint stippling of pigment. Throat stippled with grey.

COLOUR IN LIFE (based on SAM R29634): Inguinal and thigh patches flame scarlet (Smithe 1975). Ground col-

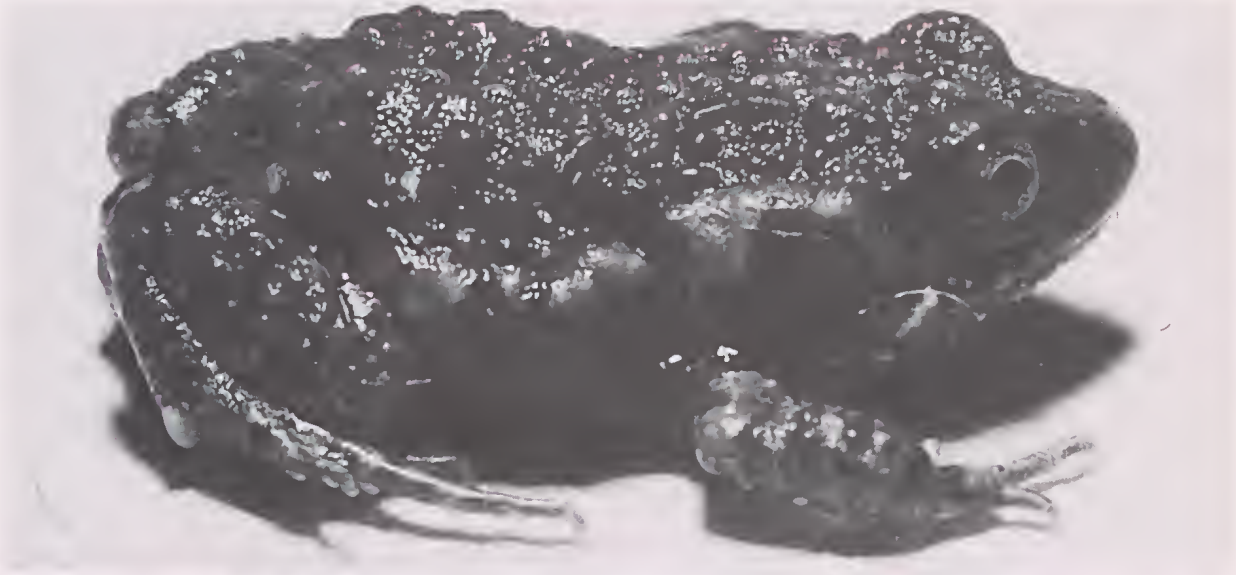

Fig. 42—*Uperoleia mimula* sp. nov. in life, Townsville Common (SAM R29634).

our dull brown with dark chocolate patches upon the head, dorsum and as narrow transverse bars across the limbs. Faint sandy patches upon the parotoids and flanks. Ventrally, densely stippled with dull grey and cream. Throat dark grey in males.

Dimensions (in mm): Snout-vent length 19.9; tibia length 6.7; eye diameter 2.3; eye to naris distance 1.5; internarial span 1.1.

Variation: There are 135 paratypes, 125 ♂♂, 7 ♀♀ and 3 subadults.

Qld: SAM R29627 (formerly QNPWS N15605), Lannercost S. F., K. R. McDonald, P. Minton, 16.ii.1984; SAM R29628, Townsville Common, B. J. Lyon, 9.iii.1977; SAM R29629-30, same locality, C. J. Limpus, K. R. McDonald, 10.ii.1977; SAM R29631-40, QM J45946, same locality, K. R. McDonald, 25.xi.1985; QM J45945, Pine River Bay, 22 km NW Rocky Point, Weipa (12°30′, 141°43′), J. W. Winter, 13.iii.1983; SAM R29641 (formerly QNPWS N28852), Bazant Outstation, Lakefield N.P., K. R. McDonald, B. J. Lyon 23.ii.1981; KU 205031, SAM R29642, Weipa, K. R. McDonald 3.iii.1981; SAM R29643, Bamaga, B. J. Lyon, C. J. Limpus 14.xii.1976; MCZ 108615, CAS 160145, AMNH 124733, SAM R29644-5, QM J45948, KU 205030, Battery Station nr Snake Creek (19°27′, 145°39′), B. C. Lawrie 3.xii.1981; QM J45944, same data, 2.xii.1981; QM J45947, Pajingo Station (20°47′, 146°11′), B. C. Lawrie 29.i.1981; SAM R29646, Base of Bluewater Range, K. R. McDonald 3.x.1983; AM R53860-1, Davies Creek Rd, Emerald Creek, 20.8 km SE Mareeba, J. Barker, G. Grigg 2.i.1974; AM R53931, 6.4 km W Herberton, J. Barker, G. Grigg 10.i.1974; AM R62684-5, R62687, Sawmill at Weipa, H. G. Cogger, E. Cameron, P. Webber 8.vii.1977; AM R46278, R46280, R46282-3, R46287, Prince of Wales Is. Torres Strait, P. Webber, E. Cameron, Young 7.ii.1975; AM R46353-92, same data 1.ii.1975; AM R46436-40, same data 11.ii.1975; AM R46460-66, same data 13.ii.1975; AM R46594, same data 15.ii.1975; AM R46931-36, R46937-43, Moa (or Banks) Is. Torres Strait, Webber, Cameron and Young 25.ii.1975; AM R46745-55, same data 21.ii.1975; AM R59167-73, Horn Is, Torres Strait, H. Heatwole, 26.xii.1976; AM R59136, same data, 25.xii.1976; QM J40234, Weipa, G. Ingram 18.iii.1982; QM J40235, J40247, SW North Camp 'Beagle' via Weipa (13°05′, 141°57′), G. Ingram 18.iii.1982; QM J42534-5, J42537, 20.8 km, W Cooktown, C. Tanner 1.vi.1974; QM J38271-2, Silver Plains Hstd (13°58′, 143°22′), J. Winter *et al.* 15.xii.1978; QM J19859, 4.8 km E Dimbulah, I. R. Straughan; SAM R29647 Lake Louisa (19°54′, 144°15′), S. Garnett 18.viii.1984.

All paratypes, with the exception of some material from Battery Station (largest measurements in ranges), are small, not very robust frogs (males 19.9-28.0 mm, females 20.9-28.4 mm) with short hind limbs [TL/S-V 0.34±0.1 (0.31-0.36)]. Eye to naris distance is usually not much greater than internarial span [E-N/IN 1.35±.19 (1.00-1.82)]. Dermal glands vary in prominence and coloration. Most of the paratypes from Torres Strait tend to have less well-developed and darker dermal glands, although they have consistently lighter-tipped tubercles on the dorsum. Many paratypes have fine suffusions of pigment on the ventral surface. Some paratypes have slightly blunter snouts than the holotype and toe fringing is slightly greater in others. Basal webbing is apparent in very few paratypes. Cream inguinal patches are well developed in many specimens. Material from Townsville Common has granular ventral skin.

Osteology (based on SAM R29641): Skull poorly ossified, sloping anteroventrally. Sphenethmoid not ossified medially; small portion ossified posteriorly to distal ⅔ of palatines and extending about ⅓ of length of orbit in ventral view. Prootic and exoccipital not fused. Exoccipital not ossified dorsomedially or ventromedially.

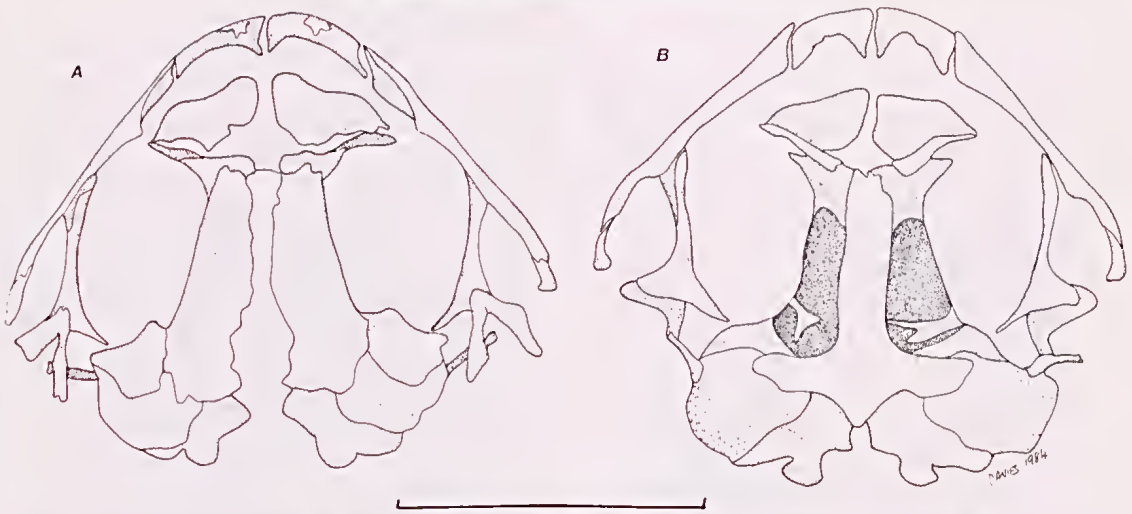

Fig. 43—*Uperoleia mimula* sp. nov. (SAM R29641). A, Dorsal and B, Ventral views of skull. Scale bar = 5 mm.

Crista parotica short, stocky, not articulating with otic ramus of squamosal. Shallow groove for carotid canal present on frontoparietals medial to prominent epiotic eminences. Anterodorsal surface of epiotic eminences expanded into small calcified protuberance. Frontoparietal fontanelle exposed for anterior ⅔ as moderately-wide slit and for posterior ⅓ as larger, incomplete, ovoid area. Anterior margin of fontanelle at level of anterior extremities of frontoparietals (Fig. 43). Posterior margin undefined because of lack of medial ossification of exoccipital. Orbital edges of frontoparietal straight, slightly angled posterolaterally.

Nasals moderately-well ossified, curved ventrally on lateral extremities and with crescentic medial anterior edge; widely separated posteromedially (Fig. 43). Nasals not in bony contact with sphenethmoid or frontoparietals. Maxillary process of nasal moderately acuminate, widely separated from well-developed preorbital process of shallow pars facialis of maxillary.

Palatines slender, slightly expanded medially, tapered laterally; reduced laterally, not extending beyond maxillary processes of nasals. Parasphenoid robust with long, moderately-slender cultriform process reaching between medial extremities of palatines. Alae moderately short, moderately slender, not overlain by medial ramus of pterygoid.

Medial ramus of pterygoid moderately long, acuminate, not in bony contact with prootic region; posterior ramus short, broad; anterior ramus expanded anteriorly, in long contact with moderately well-developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate present at base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal shaft robust, zygomatic ramus minute; otic ramus short, unexpanded.

Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes not abutting medially. Pterygoid process moderately well developed. Alary processes of premaxillaries slender, bifurcate, inclined posteromedially. Vomers absent. Bony columella present (Fig. 43).

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, poorly separated medially. Coracoids robust, moderately separated medially. Scapula bicapitate, about same length as clavicles. Suprascapula about ⅓-½ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes III > IV > sacrum > II = V = VI > VII > VIII. Urostyle bicondylar with dorsal crest extending approximately half its length. Ilial crest absent. Dorsal prominence wedge shaped, very prominent. Dorsal protuberance conical, anterolateral and prominent (Fig. 44).

Humerus with strongly-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus of six

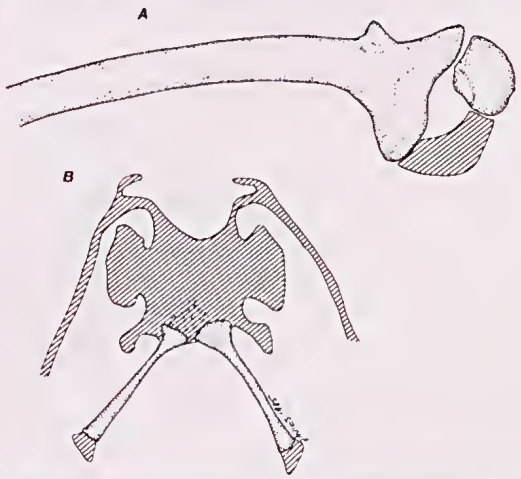

Fig. 44—*Uperoleia mimula* sp. nov. (AM R46750). A, Lateral view of pelvis. B, ventral view of hyoid.

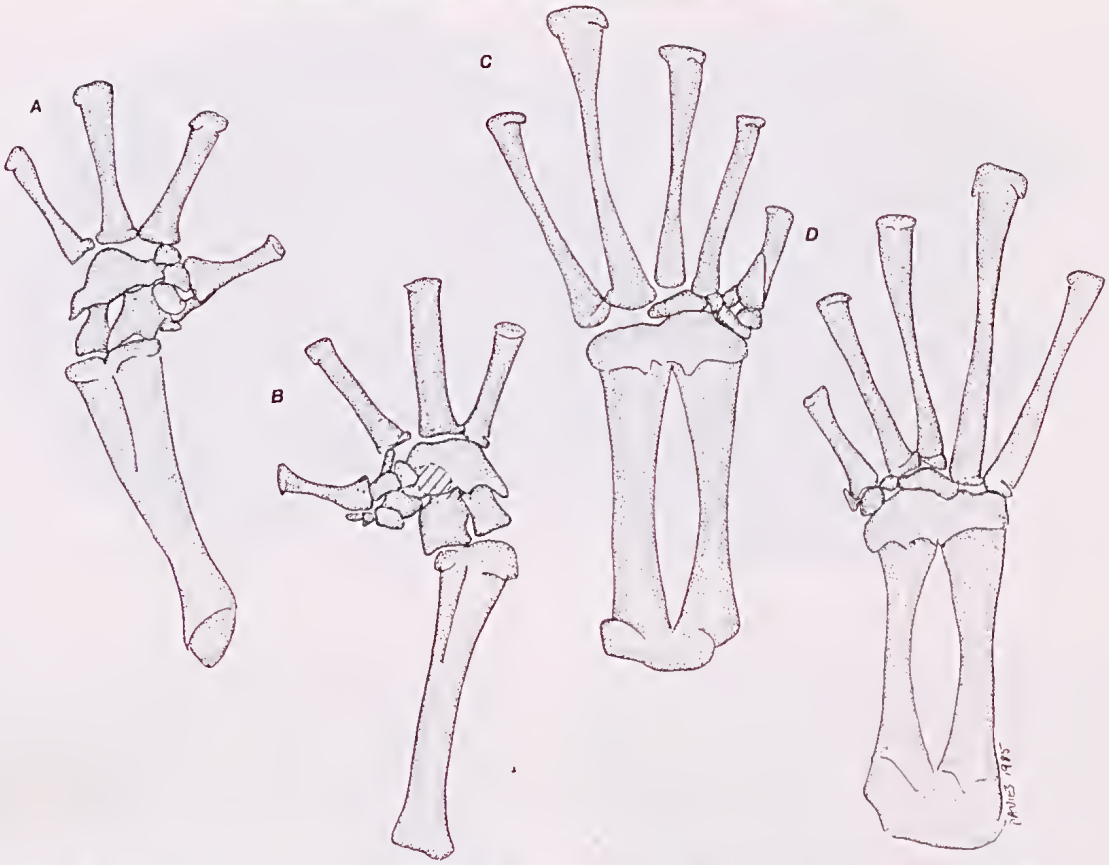

Fig. 45—*Uperoleia mimula* (SAM R29641). A, Dorsal and B, Ventral views of carpus. C, Ventral and D, Dorsal views of tarsus.

elements; considerable torsion. O. radiale and O. ulnare present. O. radiale larger of two. Both elements articulate with O. radioulna proximally and with each other proximomedially. Distally both articulate with large, transversely-elongated O. centrale preaxiale. O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Moderately well-developed flange extends proximally from lateroproximal corner. Palmar sesamoid proximomedially on ventral surface. O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal element of O. distale carpale 2, laterally with basal prepollical element. Carpal element of O. distale carpale 2 articulates with carpal element of O. distale carpale 3. Distal tips of terminal phalanges knobbed.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and O. fibulare elongate and fused at either end. O. tibiale extends as far as distal end of O. fibulare. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III and extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lying at base and slightly lateral to O. metatarsus II. Medial element lying at base of O. metatarsus I and articulating with O. centrale prehallucis (Fig. 45). Distal prehallical element large and pear shaped, extending approximately half length of O. metatarsus I (Fig. 45).

Hyoid plate approximately as long as broad. Anteromedial processes of anterior hyale slender and oriented medially. Posterolateral process of hyoid plate moderately broad and moderately short. Alary processes not pedunculate. Posterior cornua ossified. Posteromedial portion of plate slightly calcified (Fig. 44).

VARIATION: A further 23 paratypes have been cleared and stained: SAM R29642-3, R15410, R29631-3, R29645-6, QM J38271, J45947, J45948, AM R62685, R46280, R46282, R46283, R46364, R46380-1, R46437, R46746, R46932, R46934, R46390.

Three osteological features are consistent within the material examined, namely, the length and shape of the palatine processes of the premaxillaries; the length of the otic ramus of the squamosal (the shape varies occasionally with some specimens showing some expansion of the ramus); and, the tiny process on the anterodorsal surface of the epiotic eminences.

The crescentic indentation on the anterior edge of the nasals as exhibited in SAM R29641 is unique to that specimen and those from Townsville Common—all other specimens lack this feature. The shape of the pterygoid and, in particular, the slender, acuminate and acutely-angled medial process is exhibited only by SAM

R29641. The shape of the medial ramus of the pterygoid is highly variable amongst the material examined but in all cases is more robust than shown in Fig. 43.

The truncated nature of the anterior extremities of the frontoparietals is unusual, other specimens having anterolateral extensions to these bones. Exposure of the frontoparietal fontanelle varies, with very few specimens lacking the posterior expansion, but most having more crenate medial edges to the frontoparietals.

The nature of the frontoparietal fontanelle exposure is unusually variable in this species. It is poorly exposed in material from Townsville Common.

HABITAT: Found in *Melaleuca* woodland, eucalypt open woodland and woodland with tussock grassland. Frogs often shelter beneath leaf and stick litter when calling. They call from the edge of the water or up to 12 metres away.

ADVERTISEMENT CALL: The call of *U. mimula* is a short 3-5 pulsed signal with a pulse repetition rate of 75.9 sec^{-1} and a dominant frequency of 2816 Hz (see Table 3, Fig. 32).

The call is longer than, but to the ear resembles that of, the sympatric *U. lithomoda*, particularly at high temperatures (Table 3, Fig. 32). The description of the call of *Uperoleia* on Horn Island by F. Parker as a 'click' (Tyler & Davies 1984) and the close morphological similarity between *U. mimula* and *U. lithomoda* has led to the misidentification of this material.

COMPARISON WITH OTHER SPECIES: *Uperoleia mimula* is an untoothed species with a poorly- to moderately-exposed frontoparietal fontanelle, features shared only by *U. lithomoda* and *U. capitulata*.

From *U. lithomoda, U. mimula* is distinguished by a lack of strong dorsal patterning, by the presence of pigmentation on the ventral surface, by poor to moderate development of the inguinal glands and by call (the call of *U. mimula* is clearly pulsed to the ear, whereas that of *U. lithomoda* is a sharp click—see Table 3, Fig. 33).

From *U. capitulata, U. mimula* is distinguished by the absence of fringing on the fingers, a tubercular dorsum and less ossification of the nasals, and the presence of a preorbital process on the pars facialis of the maxillary.

DISTRIBUTION: *Uperoleia mimula* is confined to the Cape York Peninsula and Torres Strait Islands, extending as far south as Townsville (Fig. 46). It also occurs in New Guinea at Morchead.

ETYMOLOGY: From the Latin *mimula* meaning an actor or mimic with reference to the similarity in morphology and call of this species to its sympatric congener *U. lithomoda*.

COMMENT: Tyler and Davies (1984) assigned specimens of *U. mimula* to *U. lithomoda* on the basis of external morphology, osteology and verbal call description. Our studies have shown these two species to be difficult to separate other than on the basis of call. The specimen illustrated by Parker and Tanner (1971) from Horn Island (MCZ 80234) appears to resemble *U. lithomoda* in life (see Fig. 2). However, the preserved specimen resembles *U. mimula* in external morphology. Variation in osteology of *U. lithomoda* (see p. 148) now known to occur is a major contributing factor to misidentification of this material.

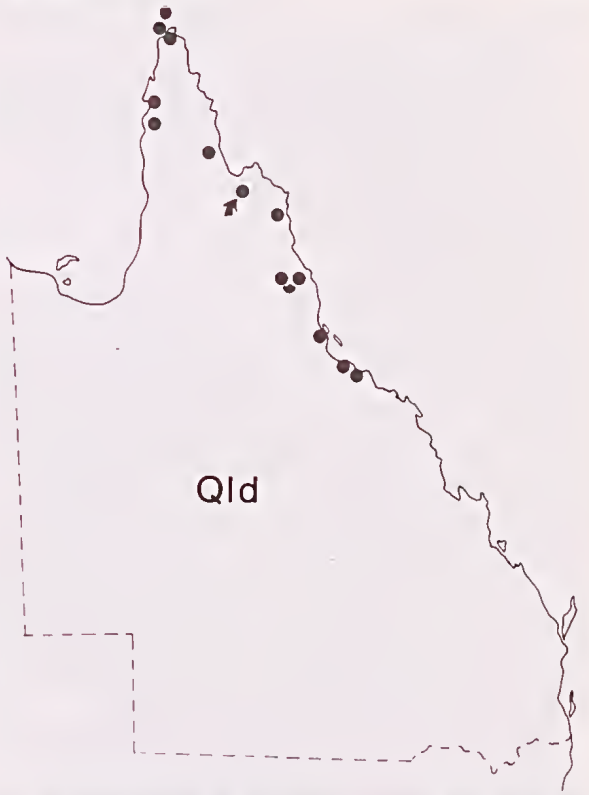

Fig. 46—Distribution of *Uperoleia mimula*. The arrow indicates the type locality.

The specimens from New Guinea examined by Tyler and Davies (1984) are osteologically closer to *U. mimula* than *U. lithomoda*. These specimens do, however, have extremely prominent inguinal and femoral patches characteristic of neither species. They are assigned here to *U. mimula* on the basis of their osteology, but excluded from the type series.

DISCUSSION

With the description of eastern Australian taxa of *Uperoleia* now largely completed, it becomes possible to examine the value of external morphology and of osteology in delimiting species in this exceptionally conservative, yet extremely speciose, genus. *Uperoleia* now comprises 23 species and it is likely that further species remain undefined.

The value of call in identifying species in *Uperoleia* has been shown by Davies and Littlejohn (1986). It is clear that *Uperoleia* contains a number of sibling species and that call data will remain essential in the elucidation of these and other taxa as yet undescribed. *Uperoleia inundata* and *U. arenicola* are separable only by call, and call is important in separating some *U. laevigata* and *U.*

fusca, U. lithomoda and *U. mimula*, and *U. tyleri* and *U. martini*.

External morphology must be used in conjunction with call data and becomes important when call data are not available. As has been shown here and elsewhere (Tyler *et al.* 1981a,b,c, Davies & Littlejohn 1986) morphology is extremely conservative in *Uperoleia* and many features show intraspecific variation necessitating an understanding of morphological variation across the range of the species.

Size has been considered a useful character in delimiting *Uperoleia* (Tyler *et al.* 1981a) and it remains so for very small and very large species. However, our data for *U. lithomoda* show size differences between different populations that, taken in isolation, could be misleading. Specimens of *U. lithomoda* on Groote Eylandt are large, larger than those from any other locality except the Lennard River region of W.A., whereas specimens of *U. lithomoda* from Edward River on the west of Cape York, are small, smaller than *U. lithomoda* from any other locality except the Mary River environs on the Arnhem Highway. The Mary River material is smaller than Amber Station and Lennard River frogs. Clearly there is no geographic cline in these data. Davies and Littlejohn (1986) noted size differences in *U. rugosa* that were associated with locality.

Size differences between species are useful in defining small species such as *U. mjobergi* (Tyler *et al.* 1981c and unpubl. data) and large species such as *U. tyleri* (Davies & Littlejohn 1986) but should be treated with caution in species with a wide geographic range.

Snout shape is considered to be a consistent species-specific character in certain Middle American hylids (Duellman, 1970) but our studies have shown variability in this feature in *Uperoleia* even at one site. Snout shape is extremely sensitive to preservation techniques and strong preservative can distort a rounded snout to the truncated condition. Thus the state of preservation of the specimen should be taken into account when examining snout shape.

Some features, such as the condition of dermal glands, show temporal variation, but the location and general extent of glands appear to be good species indicators. The function of the dermal glands is not known. The secretion from these glands may be distasteful or toxic to predators. However, examination of the stomach contents of Rufous (Nankeen) night herons (*Nycticorax caledonicus*) taken feeding on frogs at Derby airport, showed considerable numbers of *U. mjobergi* in the stomach (Tyler & Davies unpubl.). However, the other two local species, *U. talpa* and *U. aspera*, were not represented in the prey. *U. talpa* is unique amongst *Uperoleia* in that it releases copious quantities of a white frothy secretion from the parotoid glands under conditions of minimal stress. This substance is toxic to other frogs sharing the same container (Tyler, Davies, Martin & Watson unpubl.). We do not know of this phenomenon in any other species of *Uperoleia*. As indicated earlier, *Denisonia devisi* has been observed feeding on *U. capitulata*.

The activity, and thus the external appearance, of dermal glands appears to be seasonal as shown by the poor development of these features in specimens of *U. lithomoda* dug from the vegetable garden of Gibb River Station homestead during the dry season. Hypertrophy of parotoid and inguinal glands occurs in isolated specimens of most species studied, and is a feature of *U. capitulata*. Likewise hypertrophy of the parotoid glands is a feature of *U. tyleri* and *U. martini* (Davies & Littlejohn 1986).

Rugosity of the dorsum is a reliable character at the extremes of expression i.e. smooth or tubercular. Intermediate conditions are difficult to quantify. The fine conical tubercles on the dorsum of *U. trachyderma* are an excellent indicator for this species and are unique within the genus. Granularity of the ventral surface can vary, but is usually consistent. Variation may be sexual, but our data are inconclusive.

Dorsal colour patterning is a useful character provided that the limits of variability are established. Scapular plicae, golden glands, strong dark patterns or poor pattern are all species specific.

Subarticular and palmar tubercles can vary slightly. Palmar tubercles, particularly at the base of the thumb, are rarely prominent and in males are usually masked by the unpigmented glandular nuptial pad of the thumb. Supernumerary tubercles on the palm are common and vary in degree of development. Fringing on the fingers is rare and is a consistent feature in those species exhibiting it.

Toe fringing varies slightly within a species, but is generally a good character. Toe webbing is variable, but is a good feature if the extent of variability is defined. The condition of the subarticular tubercles of the toes appears constant, but is very conservative. However, the size, state and orientation of the inner and outer metatarsal tubercles can vary and in some cases these are good species indicators.

Ventral pigmentation is a reliable character. It is the only consistent feature useful in separating *U. laevigata* and *U. fusca*. It can be extremely variable in form (e.g. *U. laevigata*) or extremely constant (e.g. *U. fusca, U. tyleri, U. martini*) but recognition of the limits of variability of the feature allows its usefulness to be exploited. Colour in life of inguinal and post femoral patches is a good species indicator except in *U. fusca* where two distinct colour forms are known to occur. Unfortunately, this feature is fugitive, and is rarely recorded by collectors.

It is clear, then, that species can be grouped on a combination of morphological features, but such groupings rely heavily on knowledge of the extent of variability within any one species.

Davies and Littlejohn (1986) considered the value of osteological features in delimiting species of *Uperoleia*. In the main, our data support their conclusions. The most useful osteological feature in recognition of species in *Uperoleia* is the condition of the exposure of the frontoparietal fontanelle. However, our data on *U. lithomoda* show that this feature is subject to variation

and that ontogenetic effects must be taken into consideration. The osteological definition of a species must take account of a number of features in common, including the frontoparietal fontanelle exposure. For instance, in *U. lithomoda*, the crescentic shape of the anterior edge of the nasals and the anteromedial curvature of the orbital edges of the frontoparietals together with the poor to moderate exposure of the frontoparietal fontanelle are a combination of features unique to this species.

The condition of the distale carpalia 2 and 3 is a useful postcranial osteological feature. Three conditions occur in *Uperoleia*: the elements are fused, as in *U. rugosa, U. trachyderma* and *U. capitulata*; closely applied as in *U. tyleri, U. martini, U. fusca, U. mimula, U. littlejohni* and *U. inundata*; or, free as in *U. lithomoda* and *U. laevigata*. In those species in which the elements are closely applied, fusion occurs in isolated specimens (e.g. *U. tyleri*, Davies unpubl.).

The hyoid shows variability in the presence or absence of anteromedial processes on the anterior hyale. These processes are slender and short in all *Uperoleia* reported so far except *U. laevigata, U. fusca, U. tyleri* and *U. martini*. In these species, the processes appear to be absent and the anteromedial portion of the anterior hyale is thickened. All of these species share a dentate maxillary arch. However, the dentate northwestern species, *U. mjobergi*, has slender anteromedial processes on the anterior hyale (Davies unpubl.) and hence association of the lack of processes with dentate species occurs only in the eastern portion of the continent.

The features of the ilium appear to be species-specific and to be indicators of species relationships. The dorsal prominence has been reported as papillate in *U. glandulosa* (Davies *et al.* 1985), is tiny and rounded in *U. rugosa, U. laevigata* and *U. fusca*, is very prominent and wedgeshaped in *U. mimula* and *U. lithomoda* and monticuline in *U. tyleri, U. martini, U. trachyderma, U. capitulata* and *U. littlejohni*. The dorsal protuberance is anterolateral, lateral or posterolateral. The presence of a small ilial crest in *U. trachyderma* is unusual, a feature shared only by *U. micromeles* (Davies unpubl.).

The distribution of many species of *Uperoleia* in Queensland conforms largely to the major biogeographic boundaries proposed by Stanton and Morgan (1977). *Uperoleia littlejohni* is confined to the Desert and Einasleigh Uplands, a region that is distinctly drier, more generally elevated and more lightly timbered than Cape York Peninsula (Stanton & Morgan 1977). *U. inundata* intrudes into Queensland at Westmoreland where presumably the predominantly sparse woodland and lagoons approximate the habitat occupied by this species in coastal Northern Territory.

U. rugosa is found in the Brigalow Belt, Mulga Lands and south east Queensland region, as well as west of the Great Dividing Range in N.S.W., showing a diversity of habitat throughout its wide distribution, whereas *U. capitulata* is confined to the Mulga Lands and Channel Country complex where it is sympatric with *U. rugosa* at some sites.

U. fusca is a Central Coast Rainforest and South East Queensland species extending coastally to northern N.S.W. whereas its cryptic congener *U. laevigata* is found along the Great Dividing Range.

U. mimula, although found mainly on Cape York, has a broader habitat distribution extending to the Einasleigh Uplands and the wet tropical rainforests.

The regions of Stanton and Morgan (1977) are broadly based, and the distribution of species of *Uperoleia* within these regions is probably highly selective. *U. trachyderma* is known only from grey self-mulching cracking clays, but the association of other congeners with a particular soil type has not been documented. However, *U. lithomoda* is associated with

KEYS

Regional keys are useful in identifying material within this genus. Thus we present firstly a key to *Uperoleia* in the eastern states and then a key to the genus.

KEY TO *Uperoleia* IN EASTERN AUSTRALIA:

1. Maxillary arch dentate 2
   Maxillary arch edentate 5
2. Ventral surface fully pigmented 3
   Ventral surface never fully pigmented ..... *U. laevigata*
3. Parotoid glands hypertrophied 4
   Parotoid glands not hypertrophied ..... *U. fusca*
4. Dorsum smooth, not flecked with light pigment ..... *U. tyleri*
   Dorsum rugose, flecked with light pigment ..... *U. martini*
5. Dorsum covered with fine conical tubercles ..... *U. trachyderma*
   Dorsum not covered with fine conical tubercles 6
6. Parotoid, inguinal and coccygeal glands prominent 7
   Parotoid, inguinal and coccygeal glands not prominent 10
7. Parotoid glands hypertrophied, head small, skin relatively smooth ..... *U. capitulata*
   Parotoid glands not hypertrophied, skin rugose 8
8. Dermal glands prominently yellow tipped, providing prominent lateral stripes ..... *U. lithomoda*
   Dermal glands not prominently yellow tipped, no prominent lateral stripes 9
9. Dorsum rugose, back pattern strong, ventral surface faintly granular ..... *U. rugosa*
   Dorsum poorly rugose, back pattern weak, ventral surface smooth ..... *U. mimula*
10. Dorsal pattern discrete, tubercles pink tipped, parotoid glands rarely prominent ..... *U. littlejohni*
    Dorsal pattern never discrete, not prominent, parotoid glands prominent ..... *U. inundata*

KEY TO THE GENUS *Uperoleia* IN AUSTRALIA:

1. Internarial span less than eye to naris distance 2
   Internarial span greater than eye to naris distance ..... *U. micromeles*
2. Maxillary arch dentate 3
   Maxillary arch edentate 8
3. Prominent papilla on heel present ..... *U. mjobergi*
   Prominent papilla on heel absent 4
4. Ventral surface fully pigmented 5
   Ventral surface not fully pigmented 7
5. Parotoid glands hypertrophied 6
   Parotoid glands not hypertrophied ..... *U. fusca*
6. Dorsal surface dark, parotoid glands not pigmented ..... *U. tyleri*
   Dorsal surface flecked with light pigment, parotoid glands flecked with light pigment ... *U. martini*
7. Yellowish triangular patch on head ..... *U. laevigata*
   Greenish triangular patch on head ..... *U. marmorata*
8. Toes moderately webbed 9
   Toes unwebbed or basally webbed 12
9. Dorsal surface tubercular 10
   Dorsal surface smooth or only faintly tubercular 11
10. Parotoid glands prominent, scapular plicae present ..... *U. russelli*
    Parotoid glands moderately prominent, scapular plicae absent ..... *U. borealis*
11. Mid-vertebral stripe absent; faint dorsal pattern ..... *U. talpa*
    Mid-vertebral stripe present; no dorsal pattern ..... *U. orientalis*
12. Both inner and outer metatarsal tubercles raised and prominent 13
    Outer metatarsal tubercle small and poorly raised ..... *U. trachyderma*
13. Frontoparietal fontanelle widely exposed 14
    Frontoparietal fontanelle not widely exposed 18
14. Ventral surface unpigmented 15
    Ventral surface pigmented 16
15. Nasals moderately ossified ..... *U. inundata*
    Nasals poorly ossified ..... *U. arenicola*
16. Dorsum with strongly-developed pattern 17
    Dorsum with indistinct pattern ..... *U. crassa*
17. Toes well fringed and moderately basally webbed ..... *U. glandulosa*
    Toes poorly fringed and poorly basally unwebbed ..... *U. littlejohni*
18. Mating call a sharp click, ventral surface unpigmented 19
    Mating call a pulsed note, ventral surface pigmented 21
19. Well-developed parotoid glands and well or moderately developed inguinal and coccygeal glands 20
    Moderately developed parotoid glands, poorly developed inguinal and coccygeal glands ..... *U. minima*
20. Dorsal pattern strongly defined, inguinal glands hypertrophied ..... *U. lithomoda*
    Dorsal pattern not strongly defined, inguinal glands not hypertrophied ..... *U. aspera*
21. Frontoparietal fontanelle moderately exposed; dorsal surface faintly rugose 22
    Frontoparietal fontanelle unexposed; dorsal surface moderately rugose ..... *U. rugosa*
22. Parotoid, inguinal and coccygeal glands hypertrophied ..... *U. capitulata*
    Parotoid, inguinal and coccygeal glands not hypertrophied ..... *U. mimula*

still ephemeral waters, and *U. borealis* with streamside habitats (Tyler, Watson & Davies unpubl. data). It is likely, then, that microhabitat is extremely important in these small fossorial species.

It is probable that further species of *Uperoleia* occur in eastern Australia, but lack of collecting in particular areas and lack of call data from many specimens preclude description of these taxa at this time. The collection of *Uperoleia* is a fortuitous event—calling males are difficult to locate because of their innate ventriloquial abilities and the absence of calling activity except after rain. The size and drab appearance of foraging individuals and the long periods of time spent underground all contribute to the sparse data available on this genus, particularly from remote areas. Since many habitats are difficult, if not impossible, to visit at times of maximal frog activity, the elucidation of the boundaries of this large and morphologically conservative genus remains unknown.

CHECKLIST OF *Uperoleia* GRAY (Sequence chronological): *Uperoleia marmorata* Gray 1841
Uperoleia laevigata Keferstein 1867
Uperoleia mjobergi (Andersson, 1913)
Uperoleia rugosa (Andersson, 1916)
Uperoleia russelli (Loveridge, 1933)
Uperoleia orientalis (Parker, 1940)
Uperoleia arenicola Tyler, Davies and Martin, 1981a
Uperoleia borealis Tyler, Davies and Martin, 1981a
Uperoleia crassa Tyler, Davies and Martin, 1981a
Uperoleia inundata Tyler, Davies and Martin, 1981a
Uperoleia lithomoda Tyler, Davies and Martin, 1981a
Uperoleia micromeles Tyler, Davies and Martin, 1981a

Uperoleia minima Tyler, Davies and Martin, 1981a
Uperoleia talpa Tyler, Davies and Martin, 1981a
Uperoleia aspera Tyler, Davies and Martin, 1981b
Uperoleia trachyderma Tyler, Davies and Martin, 1981c
Uperoleia glandulosa Davies, Mahony and Roberts, 1985
Uperoleia martini Davies and Littlejohn 1986
Uperoleia tyleri Davies and Littlejohn 1986
Uperoleia capitulata sp. nov.
Uperoleia fusca sp. nov.
Uperoleia littlejohni sp. nov.
Uperoleia mimula sp. nov.

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